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REVIEW

**A NEW CLASSIFICATION OF THE GAMETOPHYTE
DEVELOPMENT OF HOMOSPOROUS FERNS, FOCUSING ON
MERISTEM BEHAVIOUR**

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ABSTRACT

Different shapes of fern gametophytes may be the result of adaptive evolution to different habitats where the gametophytes grow. In homosporous ferns, gametophytes are cordate-thalloid (terrestrial) in many taxa but can also be strap-like, ribbon-like, and filamentous (epiphytic) or tuberous (subterranean) in other taxa. Recently developed long-term observational techniques of the same individual gametophyte during growth have led to a new classification of development types for planar gametophytes. We recognise five basic types (*Lygodium*, *Elaphoglossum*, *Anemia*, *Colysis*, and *Vittaria*). The five types reflect different combinations of the three meristems: apical cell-based, marginal and multicellular meristems. In the *Lygodium*-type, the apical cell-based meristem is immediately followed by the multicellular meristem phase, resulting in typical cordate gametophytes. In the *Elaphoglossum*- and *Anemia*-types (i.e. subtypes of the *Lygodium*-type) strap-shaped and asymmetric cordate gametophytes, respectively, are formed. In the *Colysis*-type, the marginal meristem phase occurs between the apical cell-based meristem and the multicellular meristem phases, and in the *Vittaria*-type, the multicellular meristem phase is absent. In both of these latter types, irregularly branched ribbon-like gametophytes form.

INTRODUCTION

Gametophytes of homosporous ferns are generally cordate-thalloid in shape, but in some taxa they are strap-like (in e.g. Grammitidaceae, Polypodiaceae), ribbon-like (*Vittariaceae*, some of the *Hymenophyllaceae*), filamentous (some of the *Hymenophyllaceae*, *Schizaea*) or tuberous (*Ophioglossaceae*, *Psilotaceae*; Orth, 1936; Nayar and Kaur, 1971; Raghavan, 1989). The strap-like gametophyte is several times longer than broad with a cordate apex, whereas the ribbon-like gametophyte is narrow and markedly elongate, with nearly parallel sides and a round apex. The filamentous gametophyte consists of branched uniseriate filaments, and the tuberous are usually subterranean, nearly cylindrical or irregular in shape (Nayar and Kaur, 1971). Fern gametophytes are much smaller in size and have less distinguishing morphological characters than sporophytes. According to Bower (1923), the vegetative characters of fern gametophyte are deficient in stability and in variety of detail, and are consequently of minor importance in comparative studies. This general belief was unfortunate but

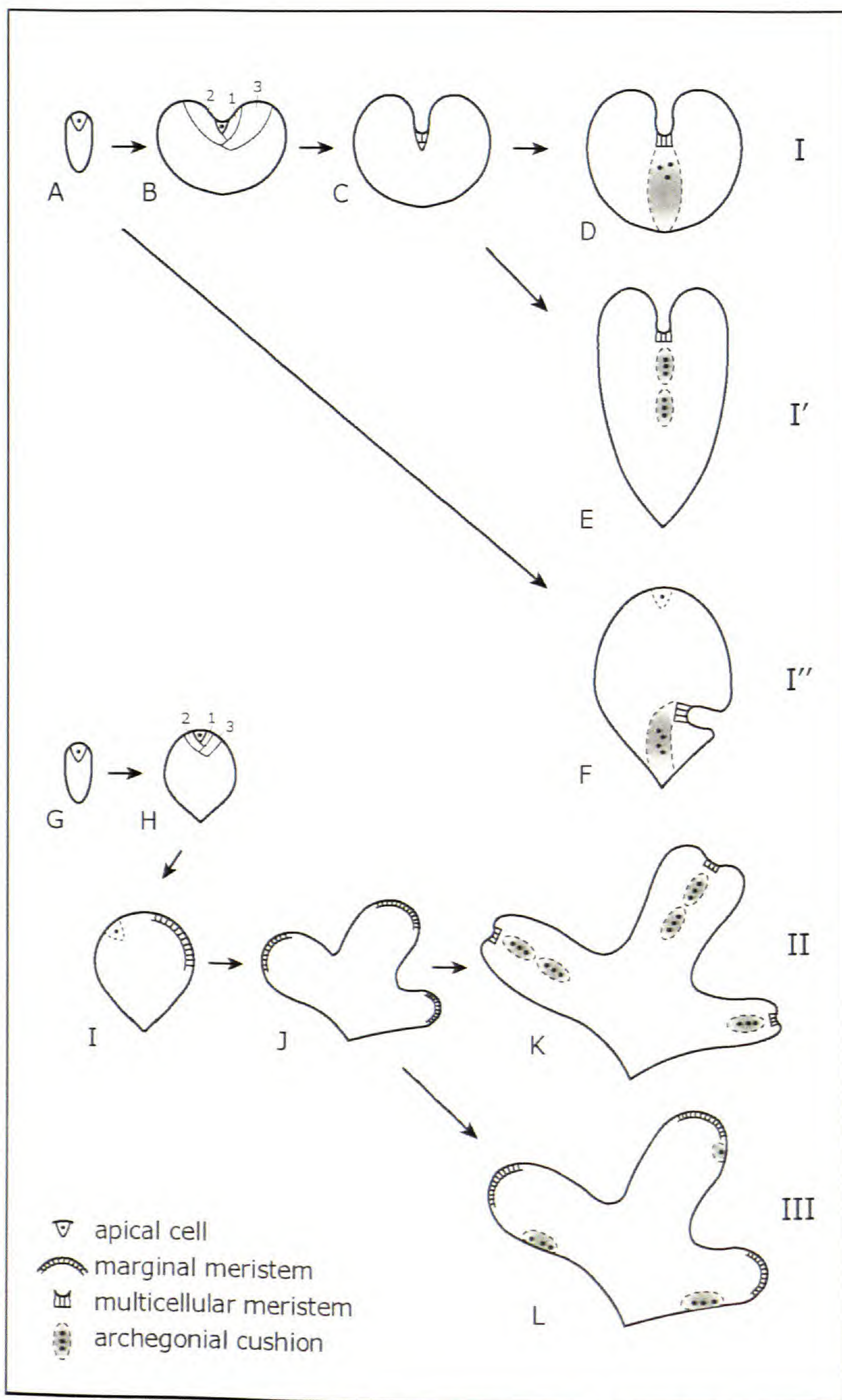


Figure 1. Diagrammatic illustrations of five developmental types of gametophytes of homosporous ferns. I, *Lygodium*-type; I', *Elaphoglossum*-type; I'', *Anemia*-type; II, *Colysis*-type; III, *Vittaria*-type. A-L indicate various stages of development. Some of the merophytes that constitute the gametophyte are shown in B and H. 1-3, the youngest to third youngest derivatives, respectively.

understandable at the time, prior to sufficient knowledge of the systematics and ecological patterns, which has now been accumulated. Since the 1950s, however, gametophyte development was targeted for research by fern taxonomists for use in classification efforts (Atkinson and Stokey, 1964), and the number of relevant publications increased (see references in Nayar and Kaur, 1971).

Based on data prior to the 1970s, Nayar and Kaur (1971) published an extensive review on the comparative development of the gametophytes of homosporous ferns, addressing the evolution of gametophyte shapes in relation to phylogeny. Various shaped gametophytes are attributable to differences in the meristem. Tuberous gametophytes have an apical meristem with either a single apical cell or a group of apical cells (Whittier, 1983; Whittier and Thomas, 1993; Takahashi and Imaichi, 2007). Filamentous gametophytes also bear an apical cell (the terminal cell) that acts as an initial cell (Nayar and Kaur, 1971). Planar gametophytes (cordate, strap- or ribbon-shaped) basically have both the apical cell and the multicellular meristem in most cases, with distinct developmental types: *Adiantum*, *Aspidium*, *Ceratopteris*, *Drynaria*, *Kaulinia*, *Marattia* and *Osmunda* (see Figure 2 in Nayar and Kaur, 1971). Since the review by Nayar and Kaur (1971), research in this field has drastically declined. Of note, however, is continued research into the remaining taxa, which is thought to be necessary for comparative study (e.g. Mendozoa-Ruiz and Pérez-García, 2005; Chou *et al.*, 2007; Gabriel y Galán and Migliaro, 2011; Testo and Watkins, 2011; references in Pérez-García and Riba, 1998).

In ferns and lycophytes, sporophytes and gametophytes are equally subjected to environmental conditions and then adapt to the habitats where they grow. To better understand the life history of ferns, recent botanists have widely accepted that information concerning gametophytes is essential (Farrar *et al.*, 2008). Field research of fern gametophytes has indicated that the life span of the gametophyte itself (annual or perennial) and its ability to reproduce vegetatively are directly related to gametophyte shape (e.g. Dassler and Farrar, 1997, 2001; Farrar, 1998; Watkins *et al.*, 2007).

As mentioned above, gametophyte shape is closely related to its life span, and the shape is a result of meristem activity. Therefore, accurate analyses of meristem behaviour are crucial for ecological as well as evolutionary studies of gametophytes. To examine meristem behaviour, Takahashi *et al.* (2009) recently conducted long-term observations of the same individual gametophyte, termed the sequential observation method. These authors captured light microscope images at set intervals (e.g. every 24 h) of the same gametophyte individual during growth, enabling an unprecedentedly easy and accurate analysis of cell lineages (cf. Figures 3 and 4 herein). Details of the methods are outlined in Takahashi *et al.* (2009). Based on meristem behaviour, five basic gametophyte types have thus far been recognised: *Lygodium*, *Elaphoglossum*, *Anemia*, *Colysis* and *Vittaria*. This classification is quite different from that proposed by Nayar and Kaur (1971). In this article, I describe these five types and discuss their developmental relationships as well as adaptation to the habitat.

Five development types

1. *Lygodium*-type (Figure 1, type I)

Previous studies have documented that the developmental process of the cordate gametophyte is quite similar among various fern taxa (references in Nayar and Kaur, 1971). At its early stage, the young narrow spatulate gametophyte forms a triangular ('obconical' or 'wedge-shaped') apical cell (Figure 1A). The apical cell produces a

limited number of derivative cells from two lateral division faces (Figure 1B) and is then replaced by the multicellular meristem (the 'pluricellular meristem' by many authors, or the 'marginal meristem' by authors before Stokey and Atkinson, 1956; Figure 1C herein). A multilayered midrib, on which archegonia arise, then develops behind the multicellular meristem (Figure 1D). The archegonial midrib is generally called the 'cushion' (Raghavan, 1989). At this stage, the gametophyte attains sexual maturity.

The commonly accepted idea that the apical cell and the multicellular meristem act as the initial cell or cells is an assumption formed by comparisons of merophyte (a clonally related cell packet) arrangements in different individuals at different developmental stages or by computer analysis (Döpp, 1927; Orth, 1936; Korn, 1974; von Aderkas and Cutter, 1983). To provide evidence for this assumption, we conducted sequential observations of the gametophyte of *Lygodium japonicum* (Thunb.) Sw. (Lygodiaceae) (Takahashi and Imaichi, in prep.), which is known to be strikingly cordate, with a deep notch overlapped by equally sized anterior wings (Momose, 1967). The apical cell of *L. japonicum* actually cuts off 6-8 derivatives in two lateral facets with a

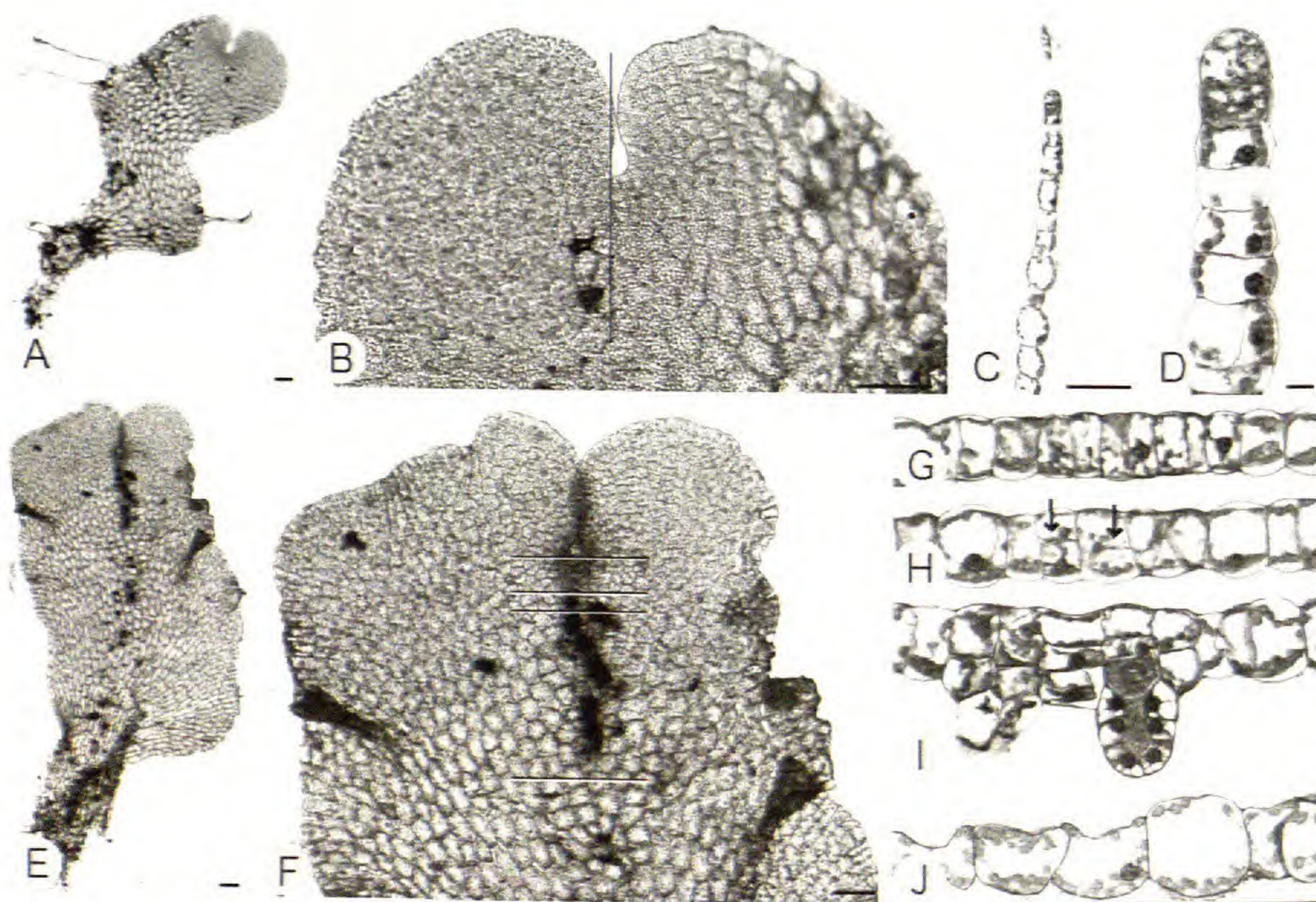


Figure 2. Gametophyte of *Selliguea hastata* (Thunb.) Fraser-Jenk. **A.** Relatively young gametophyte that has not yet developed the archegonial cushion. **B.** Enlarged figure of the apical portion of A. Vertical line indicates the site of the longitudinal section. **C, D.** Longitudinal section shown by the vertical line in B. Enlarged figure of the apical portion is shown in D. Terminal two or three cells are meristematic. **E.** Mature gametophyte with archegonial cushion. **F.** Enlarged figure of E. Four horizontal lines indicate sites of sections shown in G-J, respectively. **G.** Multicellular meristem with central narrow cells. **H.** The midrib portion that is two-cells thick. Arrows indicate cell walls formed in an orientation parallel to the substratum. **I.** Cushion with two young archegonia. **J.** One-cell layer portion below archegonial cushion. Scale bars: (A-C, E,F,J) = 100 μ m; G-J all at same magnification; (D) = 10 μ m.

left-right alternation of cell plate orientation. These derivative cells undergo repeated periclinal and anticlinal divisions to form large rectangular or fan-shaped merophytes, which are regularly arranged in a zig-zag manner and occupy most of the young gametophyte (Figure 1C). Here, the apical cell and its immediate derivatives constitute an apical meristem, called the apical cell-based meristem. After the apical cell-based meristem phase is completed, the apical cell of *L. japonicum* undergoes a transverse cell division to give rise to an anterior rectangular cell and an inner triangular cell, the former of which further undergoes anticlinal and periclinal divisions (Figure 1D), and the latter of which also divides in various orientation. In *L. japonicum*, the multicellular meristem composed of a row of 2-4 narrow cells is established at the site of the original apical cell. In this sense, the apical cell is replaced by the multicellular meristem.

The Lygodium-type of development is commonly found in cordate gametophytes of most terrestrial fern families, including Osmundaceous ferns, Gleichenioid ferns, Tree ferns, and Polypod ferns (sensu Pryer, 2004). In addition, cordate gametophytes of some epiphytic taxa, e.g. Drynarioid ferns (Polypodiaceae), also show the Lygodium-type development (Nayar, 1965; Chandra, 1979). It needs to be clarified whether cordate gametophytes of other epiphytic taxa, e.g. *Davallia* (Davalliaceae, Nayar and Kaur 1971), *Pyrrosia* (Polypodiaceae, Nayar 1961), show the Lygodium-type of development.

2. *Elaphoglossum*-type (Figure 1, Type I')

Gametophytes of epiphytic Polypodiaceous taxa often exhibit a strongly elongated, strap shape [e.g. *Elaphoglossum* (Lomariopsidaceae), and *Lepisorus*, *Christiopteris*, and *Crypsinus* (Polypodiaceae); Nayar and Kaur, 1971; Figure 1E herein]. According to the literature, the strap-shaped gametophyte also forms the apical cell and subsequently the multicellular meristem, as does the typical cordate gametophyte. However, the longer duration of the activity of the multicellular meristem compared with the typical cordate gametophyte could result in an elongated shape and a longer life span (Stokey and Atkinson, 1957 for *Elaphoglossum*; Nayar and Raza, 1970 for *Lepisorus*; Nayar, 1967b; Chiou *et al.*, 1997 for *Christiopteris*). Another characteristic to note for the strap-shaped gametophyte is that the cushion is relatively thin (2-6 cells thick for *Elaphoglossum*; Stokey and Atkinson, 1957) and is often discontinuous and intermittent (Figure 1E).

Figure 2 shows wild gametophytes of *Selliguea hastata* (Thunb.) Fraser-Jenk. (Polypodiaceae), which was growing on rocks in Kiyotaki, Kyoto, Japan. The ferns were identified using a DNA barcoding technique (Ebihara *et al.*, 2013; Ogura-Tsujita *et al.*, 2013) at the species rank. Similar to other epiphytic strap-shaped gametophytes, the *S. hastata* gametophytes are strongly elongated with a cordate apex and have marginal hairs that are reddish brown in colour (Figure 2A, B, E, F). The multicellular meristem consists of a row of narrow cells (Figure 2G), and the archegonial cushion behind the meristem is only two cells thick (Figure 2H, I). Notably, relatively young gametophytes that have already developed the multicellular meristem often do not yet have a multilayered archegonial cushion behind the meristem (Figure 2B-D). Such young gametophytes are entirely one-cell thick with no midrib. Even in mature gametophytes (Figure 2E, F), the portion below the proximal end of the central archegonial cushion is also one-cell thick (Figure 2J), perhaps indicating that the gametophyte did not produce an archegonial cushion until long after the multicellular meristem was formed. This pattern contrasts with that of the typical cordate gametophyte, in which the archegonial cushion begins to form just after the multicellular meristem is established. Such a delay in the initiation of the multilayered cushion could cause the multicellular meristem phase to be longer.

Based on the comparative development mentioned above, strap-shaped gametophytes can be regarded as a sub-type of the cordate type, i.e. highly elongated cordate gametophytes. Some intermediate shapes can be assumed to exist between the elongate-cordate and the strap-shaped gametophyte. Therefore, future sequential observations

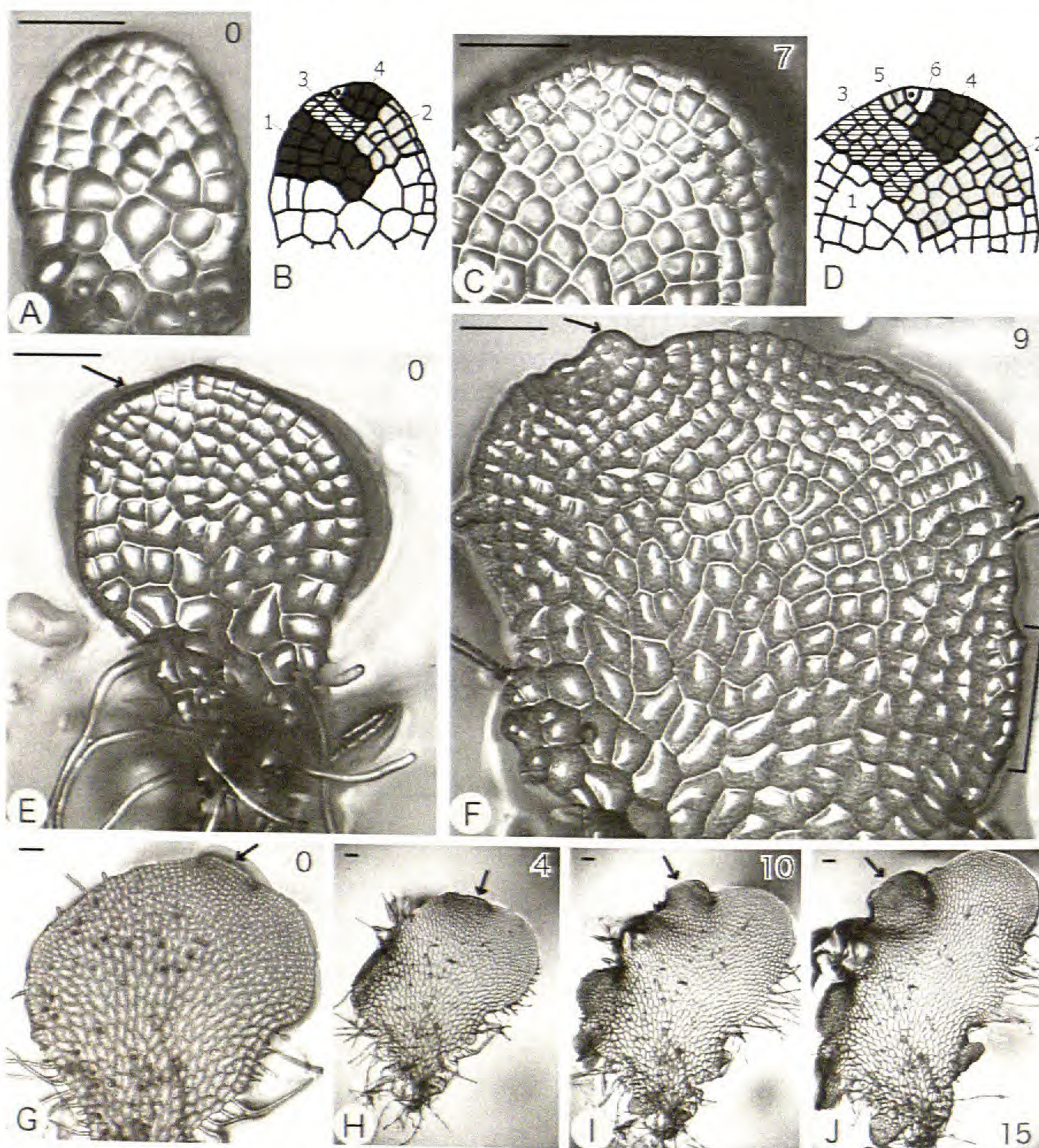


Figure 3. Gametophyte development of *Loxogramme salicifolia* (Makino) Makino. A, C, E-J. Epi-illuminated micrographs. B and D. Line drawings of A and C, respectively. Numbers at the upper (A-I) and lower (J) right corners indicate the number of days passed after observations began. **A-D.** Two early stages of the same gametophyte. Triangular cell marked by a dot regularly produces derivatives (1-6) as an apical cell. **E and F.** Two young stages of the same gametophyte. The apical cell (arrow) has stopped cell division in F. The gametophyte has been expanded in the region away from the original apical cell. The region indicated by the bracket gives rise to the marginal meristem. **G-J.** Four images of the same growing gametophyte individual at the marginal meristem stage. Arrows show the same site on the gametophyte. Due to marginal meristem activity, several lobes are growing. Scale bars = 100 μm .

should focus on the growing elongate-cordate or strap-shaped gametophytes of several taxa, including *Elaphoglossum* and *Crypsinus*.

The *Elaphoglossum*-type of development is found in epiphytic taxa of Polypodiaceae and Lomariopsidaceae.

3. *Anemia*-type (Figure 1, type I'')

In cordate gametophytes, both semicircular wings are of nearly equal size in typical cases, but they can be strongly asymmetrical with one wing larger than the other, especially when young, in some taxa such as *Anemia* and *Mohria* (Anemiaceae), *Ceratopteris* (Ceratopteridaceae), *Acrostichum* (Pteridaceae) and *Onychium* (Adiantaceae; Nayar and Kaur, 1971). In the literature, the apical cell was once reported as present (Banks *et al.*, 1993 for *Ceratopteris*), but it is typically considered to be absent (Nayar and Kaur, 1971 for the *Ceratopteris*-type; Momose, 1949; Atkinson, 1960, 1962; Pray, 1971 for *Anemia* and *Mohria*; Pal and Pal, 1963; Nayar and Kaur, 1969; Nester and Schedlbaur, 1981 for *Ceratopteris*; Nayar and Kazmi, 1964 for *Acrostichum*; Momose, 1967; Nayar and Kaur, 1971 for *Onychium*). In sequential observations of *Anemia phyllitidis* (L.) Sw., Takahashi *et al.* (2012) found that a triangular apical cell forms, as in other symmetric cordate gametophytes but, in some instances, it stops dividing just after the formation of one or, in some instances, two derivatives. Without the functional apical cell, the young gametophyte expands by intercalary growth, and a meristem with a row of narrow rectangular cells is later formed at the lateral site adjacent to the multilayered base (Figure 1F). The meristem contributes to expansion of both wings and the archegonial cushion. This meristem was once called the lateral meristem, but Takahashi *et al.* (2012) indicated that the meristem is comparable with the multicellular meristem of typical cordate gametophytes in its cell division pattern. We conclude that due to the deficiency of a functional apical cell, the initiation site of the multicellular meristem is shifted to the lateral side in the *Anemia*-type. *Ceratopteris* and *Acrostichum* also exhibit the same developmental process as the *Anemia*-type (R. Imaichi, unpublished data). In many cases, the deeply asymmetric cordate shape becomes symmetrically cordate through gametophyte growth.

The *Anemia*-type of development is commonly found in Ceratopteridaceae and Anemiaceae, and some genera of Pteridaceae and Adiantaceae.

4. *Colysis*-type (Figure 1, type II)

Some epiphytic Polypodiaceous taxa have irregularly branched gametophytes, which have been reported to be either strap-shaped (Nayar, 1962 for *Colysis* (Polypodiaceae); Takahashi *et al.*, 2009 for *Colysis*) or ribbon-shaped (Stone, 1960 for *Grammitis* and *Ctenopteris* (Grammitidaceae); Nayar, 1963 for *Leptochilus* and *Paraleptochilus* (Polypodiaceae); Nayar, 1967a for *Loxogramme* (Polypodiaceae); Wagner and Farrar, 1976 for *Hyalotricha* (Polypodiaceae) and *Grammitis* (Grammitidaceae)). The development of *Colysis decurrens* (Wall. ex Hook & Grev.) Nakaike was documented by Takahashi *et al.* (2009). Contrary to previous reports suggesting that *Colysis* gametophytes do not have single apical cells or any organised meristems (Nayar, 1962; Nayar and Kaur, 1969; the *Kaulinia* type of Nayar and Kaur, 1971), the gametophyte possesses an apical cell (Figure 1G, H) and a multicellular meristem (Figure 1K). However, the development of *Colysis* gametophytes differs greatly from that of cordate gametophytes; after the apical cell ceases to function, a new meristem (i.e. a marginal meristem; Figure 1I) arises before the multicellular meristem phase. The marginal

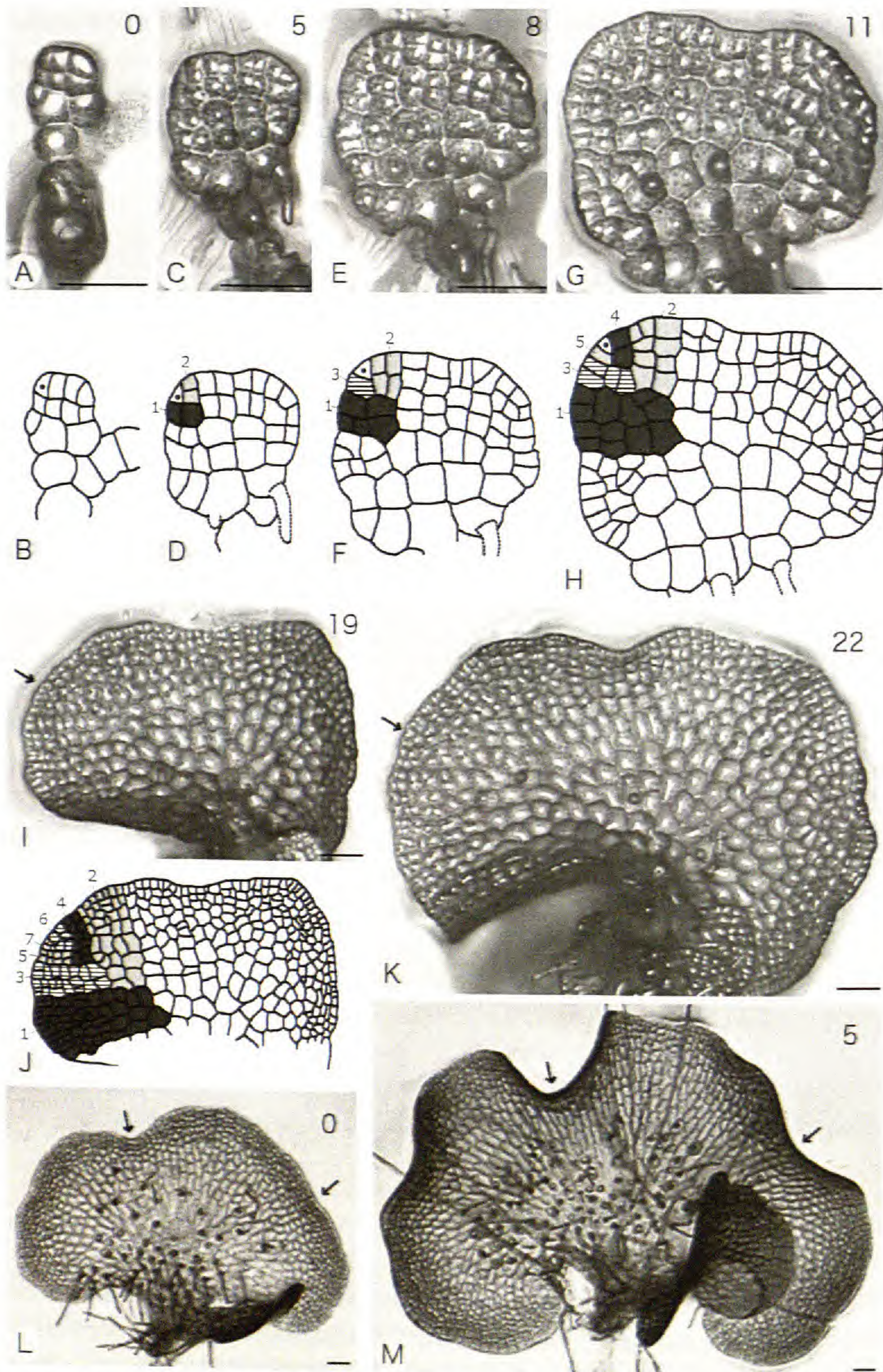


Figure 4. Development of *Vittaria* sp. A, C, E, G, I, K-M. Epi-illuminated micrographs. B, D, F, H, J. Line drawings of A, C, E, G, and I, respectively. Numbers at the upper right corners indicate the number of days passed after the observations began. **A-K.** Images at several developmental stages of the same growing gametophyte individual. Triangular cell marked by a dot indicates an apical cell. Numbers 1-9 indicate merophytes derived from the derivatives of the apical cell. Arrows in I and K indicate the site of the original apical cell. **L and M.** Two images of the same growing gametophyte at the marginal meristem stage. Left and right arrows indicate the same sites in both images where growth has been stopped. Scale bars = 100 µm.

meristem consists of small rectangular cells with no growth centre, and it covers the anterior margin of the gametophyte (Figure 1I). The marginal meristem often divides by cessation of activity in the middle, resulting in gametophyte branching (Figure 1J). During the marginal meristem phase only antheridia form, and archegonia do not arise. As a result, some strap-shaped lobes are elongated. Ultimately, a multicellular meristem is established on the anterior end of the lobe, and thin superficial cushions with archegonia are later formed (Figure 1K).

Colysis-type development also occurs in the irregularly branched gametophytes of *Loxogramme salicifolia* (Makino) Makino (Polypodiaceae). The triangular apical cell forms at the anterior end of young spatulate gametophytes. This apical cell cuts off several derivative cells and then ceases to function (Figure 3A-E). Concomitantly, cells distinct from the original apical cell become active and contribute to gametophyte growth (Figure 3E, F), and the marginal meristem occurs sporadically. In both *Colysis* and *Loxogramme*, the marginal meristem similarly develops with no relation to the original apical cell. During the marginal meristem phase, the *Loxogramme* gametophyte branches frequently to form many lobes (Figure 3G-J). No rules appear to exist in terms of branching site or frequency. During our culture period, the archegonial cushion had not yet formed in *Loxogramme* gametophytes. However, several studies have reported that the archegonia are formed on thin patchy cushions (2-4 cells thick) behind the multicellular meristem or at the anterior end in *Loxogramme* (Momose, 1967; Nayar, 1967a).

The Colysis-type of development is found in some epiphytic taxa of Polypodiaceae, and commonly found in Grammitidaceae.

5. *Vittaria*-type (Figure 1, Type III)

Another developmental type of irregularly branched gametophytes occurs in the Vittariaceae and some of the Hymenophyllaceae. Previous reports have claimed the absence of the apical cell in Vittariaceae (Nayar and Kaur, 1971), whereas the sequential observation method has documented the occurrence of an apical cell that acts as the initial cell for *Vittaria* sp. (see Figure 4). Two triangular cells are formed at the anterior end of spatulate young plates, and one of these cells is selected to be the functional apical cell (Figure 4A-D). The apical cell cuts off several (seven, in the individual observed) derivatives and ceases to divide (Figure 4D-J). After this stage, cells in the peripheral region located away from the site of the original apical cell become meristematic and gives rise to the marginal meristem (Figure 4I-K). Notably the apical cell-derived merophytes were observed to occupy only less than half of a growing gametophyte (Figure 4J). The remainder of the gametophyte grows mainly through intercalary growth. The marginal meristem then covers nearly the entire margin of the growing gametophyte (Figure 4K). The marginal meristem is involved in gametophyte branching, resulting in the production of several lobes (Figure 4L, M). After this stage, several lobes grow each to form a ribbon-like lobe, maintaining the marginal meristem at the anterior end of each lobe. In the irregularly branched gametophytes of Hymenophyllaceae, the occurrence of both a wedge-shaped apical cell and the marginal meristem has also been reported (Stokey 1940; Stone 1965).

The developmental process of Vittariaceae and Hymenophyllaceae gametophytes is similar to that of the Colysis-type up until the marginal meristem phase, as mentioned above (Figure 1 G-J). However, the location of the archegonial cushion differs greatly between the Colysis- and Vittaria-types (Figure 1 K,L). The archegonial cushion is

superficial and central in the Colysis-type, whereas it is marginal or lateral in the Vittaria-type (Farrar, 1974, 1978; Farrar *et al.*, 2008). In some taxa of Hymenophyllaceae, archegonia also arise on the two-cell-thick cushion along the margin of the thallus (Stokey, 1948 for *Hymenophyllum*; Dassler and Farrar, 1997 for *Callistopteris*), whereas in other taxa, they arise on specialised archegoniophores, which develop as lateral, or rarely terminal, outgrowths from the filaments (Stokey, 1948 for *Trichomanes*).

Figure 5 shows the irregularly branched ribbon-like gametophytes of *Hymenophyllum*

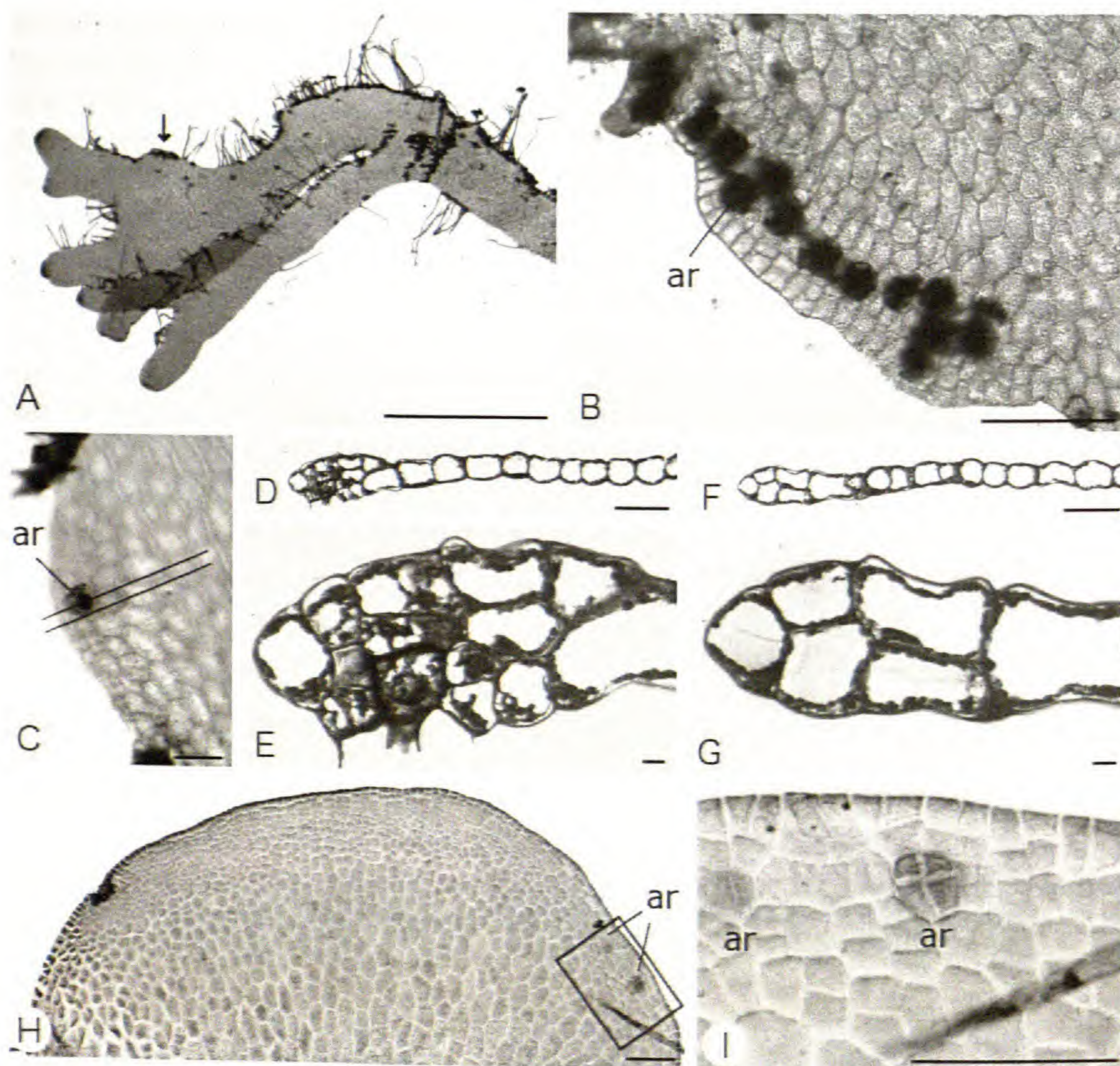


Figure 5. Wild gametophytes of *Hymenophyllum barbatum* (Bosch) Baker. A-C are light micrographs, and D-G are sectional views. H and I are light micrographs of the anterior end of a lobe, stained with Trypan blue. **A.** Irregularly branched gametophyte. Arrow indicates an archegonial cushion lobe. **B.** Enlarged figure of a marginal cushion lobe with many archegonia. **C-G.** Young lobe with an initiating archegonium. The two lines indicate sites of longitudinal sections. **D, E.** Sectional views cut at the site indicated by the upper line in C. E is an enlarged figure of archegonium-bearing region of D. **F, G.** Sectional views cut at the site indicated by the lower line in C. G is an enlarged figure of the peripheral region. **H, I.** Anterior region of a lobe covered by marginal meristem. Area demarcated by a rectangle is magnified in I. Note that newly initiating young archegonia are found in the flank of marginal meristem. ar, archegonium. Scale bars: (A-D, F, H, I) = 100 μm ; (E, G) = 10 μm .

barbatum (Bosc) Baker (collected in Okutama, Tokyo, and identified using the DNA barcoding technique). A series of archegonia appears on a marginal lobe along the basal portion of the gametophyte lobe (Figure 5A, B). The surface view of the archegonial lobe shows that it is composed of many small rectangular cells, where, unlike the multicellular meristem, a row of narrow elongate cells expected to act as initial cells cannot be distinguished (Figure 5B). Transverse sections of a young archegonial lobe show that a two-cell-thick cushion is located just behind one or two outermost cell layers that are one-cell thick (Figure 5C-G). This structure suggests that the cells just below the outermost cell layer of the marginal meristem change their division orientation from vertical to parallel to the substrate, resulting in the two- or three-cell-thick cushion. Similar changes in the orientation of cell division also occur when the archegonial cushion is formed behind the multicellular meristem in the Colysis-type.

In the surface view of the growing lobe, newly initiating archegonia are observed on the flank of the terminal marginal meristem, with the younger archegonia in the region closer to the marginal meristem (Figure 5H, I). This pattern is consistent with Stone's (1965) description: "Young archegonia were also observed on recently formed small cushion areas very close behind the apical initial cells of narrow ribbons of *Mecodium australe*....." Thus, in the Vittaria-type, the archegonial lobe probably begins to develop due to the activity of the marginal meristem. In the Colysis-type, the multicellular meristem appears to be originated from the marginal meristem, and hence the multicellular meristem is regarded as a modified marginal meristem (Takahashi *et al.*, 2009). In comparing the multicellular meristem of the Colysis-type and the marginal meristem of the Vittaria-type, the main difference distinguishing the latter from the former type lies in the site where the archegonial cushion forms (Figure 1 K,L). Notably, the archegonial cushion never forms on the marginal lobe in Colysis-type, and it never forms on central midrib in Vittaria-type, as far as we know. Future studies should more precisely compare the developmental processes of these two types.

The Vittaria-type of development is commonly found in Vittariaceae and Hymenophyllaceae.

CONCLUSION AND PERSPECTIVE

Significance of understanding development of gametophyte forms

Gametophyte biology is necessary to understand adaptation and evolution of ferns, because the gametophyte plant body (that is independent of the sporophyte plant body) is inevitably subjected to environmental conditions and then adapted to the habitats where they grow. Different habitats may select for different growth forms and different growth rates. For example, growth on a vegetation-free but temporary soil habitat is quite different from that on a long-lived tree limb in competition with bryophytes and other epiphytes. In the former habitat cordate gametophytes are generally found, while in the latter habitat slow-growing, ribbon-like gametophytes are predominant. The present review shows that such different growth forms are actually controlled by meristems. To understand gametophyte ecology and reproduction, we have to understand the gametophyte form and its basis in development.

Recent development of flora-wide barcode identification of wild gametophytes (Ebihara *et al.*, 2013; Tsujita *et al.*, 2013) helps us understand gametophyte/habitat relationships more clearly. Now gametophyte research has entered a new era involving ecological and/or evolutionary aspects. To understand the whole story of the gametophyte evolution not only the gametophyte ecology, focusing on the gametophyte-habitat

relationships, but also the comparative development, focusing on the meristem behaviour, should be investigated.

Roles of the three different meristems

Planar fern gametophytes show diversified shapes, depending on the presence or absence of the three following meristem types and how and to what extent they contribute to gametophyte development: apical cell-based meristem, marginal meristem, and multicellular meristem. Regardless of the gametophyte shape, the apical cell-based meristem is always formed as the first step of development. The apical cell-based meristem contributes to the early expansion of the gametophyte. The number of derivatives cut off from the apical cell is nearly the same among differently shaped gametophytes, i.e. 6-8 for *Lygodium* (cordate), 5-6 for *Colysis* (ribbon) and 7 for *Vittaria* (ribbon). The reason that the presence of the apical cell was previously missed in ribbon-like gametophytes (cf. Nayar and Kaur's *Kaulinia* type, 1971) is likely to be related to the shape of the anterior end of the gametophyte: it is round for the *Colysis*- and *Vittaria*-types but notched for cordate gametophytes. In the round apex of the *Colysis*- and *Vittaria*-types, each merophyte that constitutes a gametophyte is elongate-rectangular in shape (Figure 1H), whereas in the notched apex of the *Lygodium*-type, each merophyte is fan-shaped, with the longest outer margin and the shorter inner margin (Figure 1B).

The multicellular meristem has two main functions. It acts as initial cells to contribute to the expansion of both wings and formation of a multilayered archegonial cushion. In addition, the multicellular meristem is also involved in apical branching of the gametophyte. The multicellular meristem is divided into two independent meristems via the cessation of activity in the middle portion of the once extended meristem (*Lygodium japonicum*, Takahashi *et al.*, in prep.). Note that the apical cell-based meristem never divides in two.

The main role of the marginal meristem is to extend the entire periphery of the gametophyte and to contribute to the formation of many lobes through division of the marginal meristem. Owing to the marginal meristem, an irregularly branched shape is established. The marginal meristem does not contribute to the archegonial cushion in the *Colysis*-type but probably does in the *Vittaria*-type.

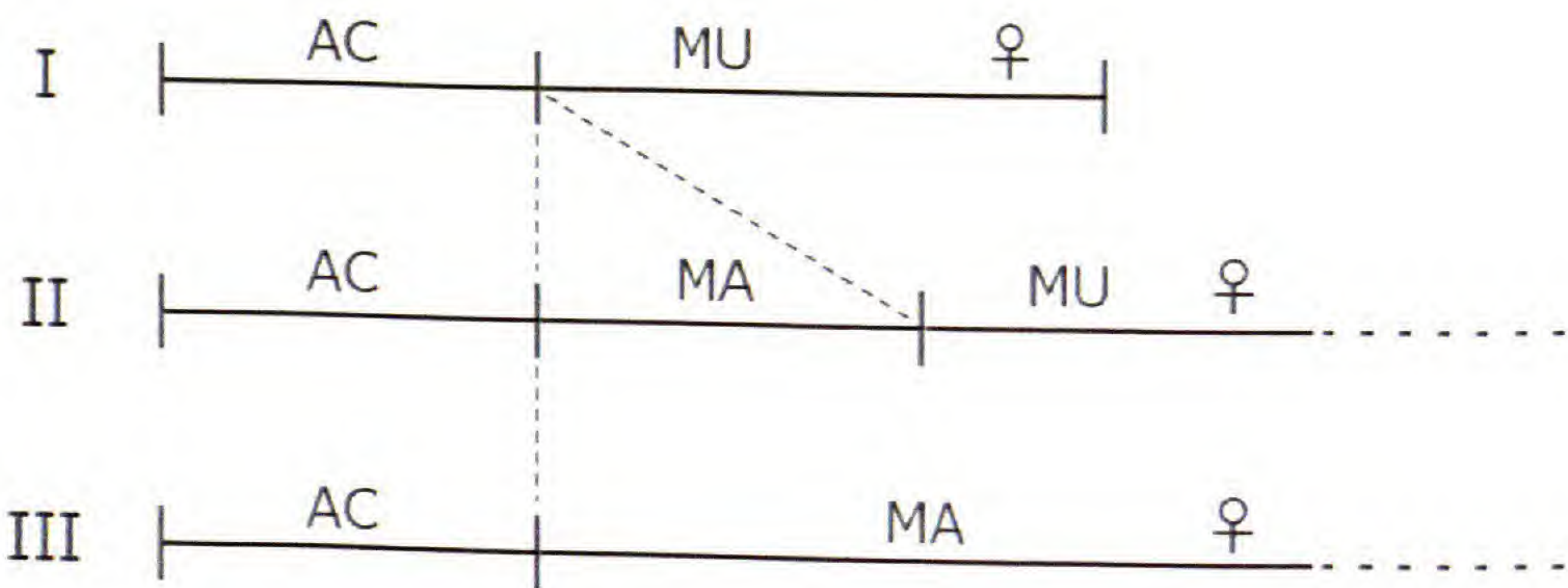


Figure 6. Diagrammatic illustrations of developmental phases that form three types. I. *Lygodium*- and *Elaphoglossum*-type for cordate gametophytes. II. *Colysis*-type. III. *Vittaria*-type. Dotted lines continuous to solid lines in II and III indicate that the multicellular and the marginal meristem phases continue indefinitely, respectively. AC, apical-cell based meristem phase; MA, marginal meristem phase; MU, multicellular meristem phase. ♀, archegonium.

Three meristem behaviours resulting in diversified gametophyte shapes

If the apical-cell based meristem phase is immediately followed by the multicellular meristem phase (Lygodium-type), the typical cordate gametophyte results (Figure 6I). In this case, the multicellular meristem begins to produce an archegonial cushion soon after the meristem is established. If the multicellular meristem does not produce the archegonial cushion for a while (i.e. the formation of the archegonial cushion is delayed; Elaphoglossum-type), a strongly elongate-cordate, strap-shaped gametophyte is formed. If the apical cell does not function and the multicellular meristem is formed on the lateral side and not on the apical end (Anemia-type), an asymmetrically cordate gametophyte results. Therefore, the Elaphoglossum-type, which forms strap-shaped gametophytes, and the Anemia-type, which forms asymmetric cordate gametophytes, are both considered to be subtypes of the Lygodium-type, which forms the typical cordate gametophyte.

If the marginal meristem phase intervenes between the apical cell-based meristem phase and the multicellular meristem phase, the Colysis-type is established (Figure 6II). During the marginal meristem phase, the gametophyte branches repeatedly, forming many lobes. This process may lead to a much longer life span of the irregularly branched gametophyte compared to the cordate gametophyte. If the multicellular meristem phase is absent, the Vittaria-type results (Figure 6III). In both the Colysis- and Vittaria-type, the gametophyte becomes irregularly branched during the marginal meristem phase. Thus, so-called ribbon-like gametophytes involve two different development types, Colysis and Vittaria. The difference between these two types involves the site of the archegonial cushion: in the former type, it is superficial and lies at the centre of the lobe, whereas in the latter type, it is located on the lateral margin of the lobe (cf. Figure 1K, L). In the Colysis-type, the archegonial cushion is formed by the activity of the multicellular meristem, which is considered modified marginal meristem (Takahashi *et al.*, 2009). In the Vittaria-type, however, the initiating archegonial lobe is found in the flank of the marginal meristem, suggesting that the marginal meristem of the Vittaria-type could have gained the ability to form a multilayered archegonial cushion near the margin because the multicellular meristem phase was lost. The developmental process of the archegonial cushion in the Colysis- and Vittaria-types should be compared further.

Farrar *et al.* (2007) classified planar fern gametophytes into three ecologically functional groups based on form, type of meristem, type of proliferation and longevity: annual cordate gametophytes with the meristem in the notch, perennial strap-shaped with the meristem in the notch and perennial ribbon-shaped that have the meristem in the margin. Missing from this classification is the Colysis-type, which has meristem in both the margin (marginal meristem) and the notch (multicellular meristem). Still other types of development may also occur, especially for irregularly branched, ribbon-like gametophytes. For example, the very narrow gametophytes of *Pleurosoriopsis* (Polypodiaceae) appear always to retain the triangular apical cell and have superficial archegonial cushions (Masuyama, 1975; R. Imaichi, personal observation). Gametophytes of *Phanerosorus* (Matoniaceae) are also ribbon-shaped with an apical cell and a superficial archegonial cushion (Yoroi and Kato, 1987). Whether these gametophytes possess the multicellular meristem when the archegonial cushion forms remains uncertain. In some *Trichomanes* (Hymenophyllaceae) species, the gametophyte uniquely shows two sharply defined growth forms: a filamentous, branching phase that gives rise to an upright, blade-like phase (Farrar and Wagner, 1968 for *Trichomanes*).

The examination of gametophyte development should be especially extended to non-cordate gametophytes that mainly occur in epiphytic taxa.

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A SHORT BIOGRAPHY



RYOKO IMAICHI received her doctoral degree from the Botany Department of Kyoto University in 1983. She was appointed as a Research Associate of the Faculty of Agriculture of Tamagawa University in 1977, Associate Professor in 1987, and Professor in 1995. Since 1997, she has been a Professor of the Faculty of Science of Japan Women's University. Dr Imaichi is affiliated with the Botanical Society of Japan; Japan Society of Plant Taxonomists; Japanese Society of Plant Morphology; the International Association of Pteridologists and the Botanical Society of America.

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THE GENUS *ADIANTUM* L. FROM MAHARASHTRA: A NOTE ON THE ADDITION OF TWO SPECIES FOR MAHARASHTRA, INDIA

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Key words: *Adiantum concinnum*, *A. poiretii*, Western Ghats, Maharashtra.

ABSTRACT

The genus *Adiantum* L. from Maharashtra is revised; seven species are recognized. *Adiantum concinnum* Willd. and *A. poiretii* Wikstr. are new records for Maharashtra, and are described and illustrated.

INTRODUCTION

The genus *Adiantum* is a large genus of some 280 species globally, with 20 species and two varieties reported for India. The Western Ghats of India has 10 species of *Adiantum*, of which five species have been reported previously from Maharashtra (Blatter and d'Almedia, 1922). The present investigation was undertaken to study the genus *Adiantum* from Western Ghats of Maharashtra. Seven species of *Adiantum* were found, with two species, *A. concinnum* Willd. and *A. poiretii* Wikstr., being recorded for the first time for Maharashtra State.

MATERIALS AND METHODS

Field visits were carried out from June 2010 to December 2012 for the collection of *Adiantum* species from Northern Western Ghats. The specimens are preserved in the Herbarium, Department of Botany, Shivaji University, Kolhapur (SUK) and were identified by using the floristic accounts of Beddome (1884), Blatter and d'Almedia (1922), Dixit (1984), Manickam and Irudayaraj (1992) and Fraser-Jenkins (2008).

RESULTS AND DISCUSSION

Taxonomic Treatment

Adiantum L. Sp. Pl., 1094 (1753); Copland, Gen. Fil. 78, 1947; Beddome, Ferns S. Ind., 1 (1970); Almedia, Cont. Stu. Vas. Pl. Mah. Rev. Pterido., 140, 1972; Manickam & Irudayaraj, S. Ind. Pterido., 95, 1994. Type - *Adiantum capillus-veneris*, United States, Holmiea.

Hewardia J. Sm., J. Bot. (Hooker) 3: 432. 1841.

Rhizome erect or creeping, densely or sparsely covered with scales; *scales* uniform or differential, multicellular, dark brown 1 - 3 mm long; *stipe* 5 - 15 cm long, dark brown, glabrous or hairy; *lamina* simply pinnate to tripinnate or quadripinnate (*A. raddianum* Presl.); *pinnule* herbaceous 2 - 3 cm long, dark green to pale green, usually dimidiate, glabrous or hairy (*A. caudatum* L.); *veins* free, dichotomously branched, reaching up to margin; *sori* marginal or borne in the notches, reniform to linear; *spores* trilete, and granulose.

Key to the species

- 1a. Fronds once pinnate 2
 1b. Frond pinnately branched, glabrous 4
 2a. Fronds rooting through apical buds 3
 2b. Frond is not rooting through apical buds; pinnae glabrous *A. incisum*
 3a. Pinnae densely hairy *A. caudatum*
 3b. Pinnae glabrous *A. philippense*
 4a. Rhizome erect, pinnules pale green *A. concinnum*
 4b. Rhizome creeping, pinnules dark green 5
 5a. Pinnules semicircular *A. poiretii*
 5b. Pinnules dimidiate or sub-dimidiate 6
 6a. Rhizome short creeping, lamina deltoid, tripinnate *A. raddianum*
 6b. Rhizome long creeping, lamina bipinnate *A. capillus-veneris*

Adiantum concinnum Willd., Sp., 5.451(1810); Mickel & Beitel, Pterid. Fl. Oaxaca, Mexico, 23, Figure 38 K.L. (1988); Beddome, Ferns S. Ind., 1 (1970); Almedia, Cont. Stu. Vas. Pl. Mah. Rev. Pterido., 140, 1972; Manickam & Irudayaraj, S. Ind. Pterido., 95, 1994. Type - Venezuela, Caracas, Cumana.

Adiantum lutescens Moug. ex Fee, Mem. foug 5: 119 (1852).

Adiantum concinnum var. *subvolubile* Mett. Lehmann, mid, J, P40.

Rhizome erect or suberect, densely scaly at apical part; *scales* \pm 5 mm long, 0.2 - 0.4 mm wide, lanceolate, apex acuminate, margin entire; *stipe* 15 - 28 cm long, smooth, glabrous, slender, tufted, scaly at base, dark brown, abaxially rounded, slightly grooved adaxially; *frond* 40 - 50 cm long, 15 - 25 cm broad, bipinnate to tripinnate, triangular or ovate, apex acute, base broadly cuneate; *pinnae* thin, herbaceous, Primary pinnae 8 - 12 pairs, alternate, short stalked, terminal pinnule similar to lateral, Secondary pinnae stalked, base oblique, pinnules 3 - 5 pairs per secondary pinnae, shortly stalked, fan shaped, ovate or wedge shaped, base truncate, margin deeply lobed into 2 - 3 primary lobes; *veins* dichotomously branched, springing from the base and freely reaching towards the margin; *pinnae* pale to dark green, glabrous, above and below, texture thin herbaceous; *sori* kidney shaped, 8 - 15 on each pinnules, exindusiate, papery; *spores* diam. 30 - 38 μ m, tetrahedral, exine red-brown, granulose (Figure 1).

Distribution and Ecology: Rare along exposed road sides and road cuttings from Panhala Hill station between altitude 900 - 1000 m. The species is an escape from C. and S. America, and is now naturalised in South India and North East Himalaya.

Note: *A. concinnum* is reported here for the first time as a new record for Maharashtra State.

Adiantum poiretii Wikstr. Kongl. Vetensk. Acad. Handl. 1825. 443. 1826; Fraser-Jenkins, Tax. Rev. Three Hund. Ind. Subcont. Pterid. 577, 2008. Type - Tristan Da Cunha

Adiantum crenatum Baker., Syn. Fil. (Hooker & Baker) 120. 1867.

Adiantum gratum Fée., Mém. Foug., 5. Gen. Filic. 119. 1850-52; 7 mem. 29 t. 12 f. 3. 1850.

Adiantum poiretii var. *sulphureum* (Kaulf.) R.M. Tryon. Amer. Fern J. 47: 139. 1957.

Adiantum sulphureum Kaulf. Enum. Filic. 207. 1824

Adiantum sulphureum. var. *subsulphureum* (J. Rémy ex Gay) Looser. Physis (Buenos Aires) 15: 225. 1939.

Rhizome creeping, \pm 5 mm dia., scaly at base; *scales* 5 mm long 0.7 - 1 mm wide,

filiform, thin, hair like, yellowish brown, broadly triangular, margin entire, apex acuminate; *stipe* 8 - 15 cm long, lustrous, glabrous, red-brown, bearing conspicuous basal scales, similar to those of the rhizome; *frond* 20 - 25 cm long, 12 - 14 cm wide, thin herbaceous, deltoid, bipinnate or tripinnate, ovate, apex acute base cuneate; *pinnules* herbaceous, suborbicular, fan shaped, lobed half way to the base, base cuneate or rounded, non soral margin crenulate; *veins* dichotomously branched, forked three to five times, free reaching up to margin, springing from cuneate base; *sori* linear, exindusiate, marginal in between notches, 1 - 2 per lobe; *spores* dia. 34.6 - 53.6 μ m, trilete, exine smooth (Figure 2).

Distribution and Ecology: Rare in Western Ghats of Maharashtra, found in Panchagani on wet rocks or wall near the roadside at an altitude of 1000 m. It is associated with



Figure 1: *Adiantum concinnum* Willd. **a:** Habitat **b:** Rhizome **c:** Enlarged pinna **d:** Pinnae showing sori and venation.

Cheilanthes rufa D. Don., *Microsorium membranaceum* (D. Don) Ching. and *Hypodematum crenatum* (Forsk.) Kuhn.

Note: This species is reported here for the first time from Maharashtra State.

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Figure 2: *Adiantum poiretii* Wikstr. **a:** Habitat **b:** Rhizome **c:** Rhizome scale **d:** Pinnae showing sori and venation.

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GLAZIOU'S PTERIDOPHYTE COLLECTION AT THE PARIS HERBARIUM

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Key words: Pteridophyta, Herbarium MNHN Paris, Glaziou, Appun.

ABSTRACT

During our work on pteridophytes for the 'Flora of the Guianas' programme, we have examined specimens from numerous herbaria, and especially from Paris (P). We have realised the importance of Glaziou's collection which is deposited at P. The detailed study of this collection led us to point out the difficulties of interpretation of dates and localities given on the labels of this collection. Therefore, for the benefit of further users of this collection, a complete inventory is being carried out. Examination of the collection catalogue, specimens, literature and associated databases has allowed the comparison of the labels and establishment of the chronology of the specimens and of the sites of collection. We have also studied Appun's collections from Guyana; these specimens were given by Appun to Glaziou, who incorporated them within his numbering. This paper presents the preliminary results of our study. However, after some five years of works for the installation of compactors for the Paris herbarium collections, and including mounting, digitising and re-curation of the pteridophyte specimens, these are once more accessible for research and all specimens will need a new revision.

Mots clés : Ptéridophytes, Herbar MNHN Paris, Glaziou, Appun.

RÉSUMÉ

Lors de nos travaux sur les Ptéridophytes pour le programme 'Flora of the Guianas', nous avons examiné les spécimens de nombreux herbiers, et plus spécialement celui de Paris (P). Nous avons ainsi remarqué l'importance de la collection d'A.F.M. Glaziou déposée à P. L'étude de détail de cette collection nous a permis de constater les difficultés d'interprétation des dates et des lieux de récolte portés sur les étiquettes des spécimens de cette collection. Aussi, pour le bénéfice des utilisateurs ultérieurs de cette collection, en avons-nous entrepris un inventaire complet, actuellement toujours en cours. L'examen des carnets de récolte, des spécimens, de la bibliographie et des bases de données nous a permis de comparer les étiquettes et d'établir la chronologie des spécimens et des lieux de récolte. Cet article présente les résultats préliminaires de notre étude. Toutefois, la collection de l'herbier de Paris nécessite une nouvelle révision, du fait des travaux de rénovation de l'herbier, tous les spécimens étant désormais

accessibles. Nous avons également étudié les récoltes d'Appun du Guyana. Ces spécimens ont été donnés par Appun à Glaziou qui les a intégrés dans sa numérotation.

INTRODUCTION

In the course of our research on American pteridophytes for the 'Flora of the Guianas' international programme, and the 'Index of American Pteridophytes', we have looked for specimens collected from the three Guianas (Guyana, Suriname, French Guiana), as well as for type specimens.

We have observed that:

Glaziou's pteridophyte collection in Paris (P), mainly studied by A.L.A. Fée (1869, 1872-1873) and by J.G. Baker (1870), contains a great number of taxa new at this time and described by these two authors;

A certain number of specimens from this collection were collected in Brazil by amateurs and other botanists, but also collected in Guyana by C.F. Appun.

François-Marie Auguste Glaziou was born in Lannion (Côtes-d'Armor, France) on August 28th, 1828 of an 'unknown father'. In February 1834 his mother, Marie-Joseph Grosvalet, married Yves Glaziou, a gardener-horticulturist, who recognised him and gave him his name. At 16 years of age, he escaped from home to make a tour of France, but stopped at Bordeaux. A good horticulturist, he applied himself to botany and the art of gardening. He married, fathered a family, and in 1859 set sail for Brazil as a migrant. In 1862, he was engaged to create several gardens in Rio de Janeiro. At this period, C.F.P. von Martius (1794-1868) had undertaken the writing of '*Flora brasiliensis*' and needed correspondents in Brazil. Glaziou became involved in the important task of plant collecting from unexplored areas. He considered knowledge to be universal, and sent specimens of plants to many herbaria in Europe and in South America. His collections of lichens and mosses allowed A.L. Fée (1789-1874) to publish a flora of the Cryptogams of Brazil in 1869. In 1897, tired and sick, he took retirement and returned to France where he stayed close to Bordeaux. He spent the remaining years sorting out his herbarium and his documents until his death in 1906 (after Allain 2008).

We have now started the inventory of all Glaziou's specimens deposited at the National Museum of Natural History in Paris (P). We supplemented the data by including information from databases of various herbaria (B, BM, BR, C, G, K, MO, NY, P, RB, US). These databases were revealed to be incomplete, as entry of specimen data is still in progress. Our study of Glaziou's specimens has started with the examination of his catalogue of collections, then the literature.

Our study of this collection revealed to us the difficulties of interpretation of the information shown on Glaziou's labels. It is also known that Glaziou had collected certain plants at various periods, but referred to them under the same number. Through the inventory and the bibliographical information, we have been able to draw preliminary conclusions that we present here.

GLAZIOU'S COLLECTION CATALOGUE

Glaziou's collection catalogue, deposited at the library of the Paris herbarium (P), consists of 3 registers noted as "carnets de récoltes" (collection notebooks) which are not true field books but rather a listing of the collection numbers, in which the information is very minimal. For each of the 26,000 records only a number and the name of the plant are indicated. From our records a total of some 1,789 of these

numbers correspond to pteridophytes. The information in this catalogue is presented in the following style:

- 362 *Acrostichum consobrinum* Kunze
 363 *Ceropteris tartarea* Link
 364 *Mertensia sculpturata* Fée
 365 *Mertensia pubescens* Humb. & Bonpl.
 366 *Mertensia pubescens* Humb. & Bonpl.
 etc.

GLAZIOU'S COLLECTION

Using this list of pteridophyte specimens given by Glaziou in his collection catalogue, we have looked for the specimens deposited at P. The information shown on the specimen labels has been recorded, together with information found in the literature. There is variation in the type of information from one specimen label to another. The list below provides examples of the various categories of these labels, with the current name of the taxon given for each Glaziou number.

Case 1

This is the simplest category:

364 Catalogue: *Mertensia sculpturata* Fée

Specimen label: Rio de Janeiro: (syn- P00633236!) [det. as *Dicranopteris flexuosa* (Schrad.) Underw. by S. Roth in 1985].

Syntype of *Mertensia sculpturata* Fée, Crypt. Vasc. Brés. 1: 199, t.72, f.1. 1869.

Protologue: “*Habitat in Brasilia fluminensi* (Claussen, n° 102 a [Herb. F.]; Glaziou, n° 364, et 1695)”.

Current name: *Dicranopteris flexuosa* (Schrad.) Underw. [fide Lellinger 1989, Andersen & Øllgaard 2001].

Case 2

When naming Glaziou's specimens, it happens that several authors did not give the same name for a specimen. The names given now become synonyms of the current name of the taxon.

378 Catalogue: *Alsophila scrobiculata* Fée

Specimen label: Rio de Janeiro: Corcovado, 12 Jan 1867 (syn- P00631754!; isosyn-BR!, P00631755!, P00631756!).

Syntype of *Alsophila scrobiculata* Fée, Crypt. vasc. Brés. 1: 157, t.53, f.1. 1869.

Protologue: “*Habitat in Brasilia fluminensis* (Glaziou, n° 378, 2293, 2294, et 2295) ”.

In : *Alsophila paleolata* Mart. [Fl. Bras. 1(2): 329. 1870].

Current name: *Cyathea phalerata* Mart. [fide Zuloaga *et al.* 2008, Forzza *et al.* 2012].

Case 3

Sometimes, the same number is indicated for different taxa and, very occasionally, for different dates. But, the collection dates are not always reported on the specimens, and notably never on the duplicate specimens. A specimen number shown on the herbarium sheet can only be related to the numbers in the catalogue when dates are indicated on the specimens, and that is extremely rare.

1221 Catalogue: *Goniophlebium lepidopteris* T. Moore

a) Specimen label: Rio de Janeiro: in sands of Talupu, 18 Jun 1867 (P01374808!)

Goniophlebium lepidopteris T. Moore, *Acrostichum lepidopteris* Langsd. & Fisch.

In : *Goniophlebium lepidopteris* T. Moore [Crypt. Vasc. Brés. 1869.]

Current name: *Pleopeltis lepidopteris* (Langsd. & Fisch.) de la Sota [fide Sota 2007].

b) Specimen label: Rio de Janeiro: (syn- P00167446!; isosyn- NY148808-fragm.).

Syntype of *Alsophila tijucensis* Fée, Crypt. vasc. Bres. 1: 171, t.73, f.1. 1869.

Protologue : “*Habitat in Brasilia fluminensis, ad Tijuca* (Glaziou, n° 1221, et 1707).”

Current name: *Cyathea poeppigii* (Hook.) Domin [fide Lellinger 1989, Forzza *et al.* 2010].

c) Specimen label: Rio de Janeiro

In : *Dicksonia cicutaria* Sw. [Crypt. Vasc. Brés. 1869.]

Current name: *Dennstaedtia cicutaria* (Sw.) T. Moore [fide Sota 1977, Smith 1981, Stolze 1981, Proctor 1985, Mickel & Beitel 1988, Proctor 1989, Tryon & Stolze 1989, Mickel 1992, Moran & Riba 1995, Mickel & Smith 2004, Zuloaga *et al.* 2008].

d) The Glaziou number 1221 is also cited by Baker, Fl. Bras 1(2): 527. 1870.

- *Polypodium lepidopteris* (Langsd. & Fischer) Kunze var. *rufulum* (C. Presl) Baker

Current name: *Pleopeltis hirsutissima* (Raddi) de la Sota [fide Zuloaga *et al.* 2008].

Case 4

Two specimens collected at different dates are indicated under the same number. As an example, we present here number 1680, but this applies also for numbers 424 and 917.

1680 Catalogue: *Aspidium amaurolepis* Fée

a) Specimen label: Rio de Janeiro: Serra dos Órgãos, Tijuca, 8 Aug 1867 (syn-P00170065!; isosyn- C, P001415573!, US!).

Syntype of *Aspidium amaurolepis* Fée, Crypt. vasc. Bres. 1: 137, t.44, f.2. 1869.

Protologue: “*Habitat in Brasilia fluminensis* (Glaziou, n° 1680, a Tijuca, et 2370, 2371, 2372).”

Current name: *Ctenitis distans* (Brack.) Ching

For Baker [Fl. Bras. 1(2): 472. 1870] this specimen corresponds to *Nephrodium caripense* (Willd.) Hooker

Current name: *Ctenitis submarginalis* (Langsd. & Fischer) Ching [fide Sota 1977, Stolze 1981, Zuloaga 1997, Zuloaga *et al.* 2008].

b) Specimen label: Rio de Janeiro: Corcovado, 8 Sep 1867 (P01592212!, P01592213!, P01592214!, P01592215!)

Gymnotheca polyodon Presl

Current name: *Marattia cicutifolia* Kaulf. [det. Christenhusz 2006]

Case 5

Appun's specimens, collected in Guyana and given to Glaziou, are integrated within the numbering of Glaziou's collection. For the other gifts of specimens, it is extremely rare that they are mentioned in the collection catalogue:

12347 Catalogue: *Blechnum asplenioides* Sw.

Specimen label: GUYANA: Appun s.n. (P01532127!)

Blechnum asplenioides Sw.

Current name: *Blechnum asplenioides* Sw. [fide Murillo 1968, Sehnem 1968, Kramer 1978, Cremers & Hoff 1990, Tryon & Stolze 1993, Smith 1995, Killeen & Schulenberg 1998, Forzza *et al.* 2010].

Case 6

Numerous specimens are without number:

In the description of taxa, the author mentions "Glaziou s.n.", as in this case, here below, for a Christ species.

This is correct and conforms to the protologue.

s.n. (holo- P00559058!).

Type of *Lycopodium alopecuroides* var. *pseudo-reflexum* H. Christ, Bull. Herb. Boiss. ser. 2, 2: 706. 1902. [det. as *Lycopodiella alopecuroides* (L.) Cranfill var. *integerrima* (Spring) B. Øllg. & P.G. Windisch by B. Øllgaard and P.G. Windisch in 1993]

Protologue: "Glaz. s.n."

Current name: *Lycopodiella longipes* (Hook. & Grev.) Holub [fide Arana & Øllgaard 2012]

In most cases, the number is frequently omitted on the label. This is the case for a number of duplicates. However, thanks to the indication of location and date of collection, it is possible to extrapolate and to estimate a probable number for the specimen.

s.n. Petropolis, 16 Feb 1866 (P01227946!) [prob. n° 913]

Lycopodium complanatum L.

Current name: *Diphasiastrum thyoides* (Humb. & Bonpl. ex Willd.) Holub [fide Arana & Øllgaard 2012].

Case 7

By comparison of the numbers mentioned in the collection catalogue and the numbers found on the specimens, we have established that there are a further 75 additional numbers:

- either with a name belonging to a Phanerogam, but with a specimen being a pteridophyte:

11 Catalogue: *Scoparia dulcis* L. [Scrophulariaceae]

Specimen label: Rio de Janeiro : Alto Macahé, Jul 1870 (P01541570!)

Heteroneuron serratifolium (Mert. ex Kaulf.) Fée

Current name: *Bolbitis serratifolia* (Mert. ex. Kaulf.) Schott [fide Sota 1977, Sehnem 1979, Smith 1981, Tryon & Stolze 1991, Smith 1995, Kessler *et al.* 2000, Mickel & Smith 2004, Funk *et al.* 2007, Hokche *et al.* 2008].

- or without name, but with a specimen being a pteridophyte:

248 Catalogue: No indication.

Specimen label: (P01224203!)

Lycopodium reflexum Lam. [det. B. Øllgaard 1987]

Current name: *Phlegmariurus reflexus* (Lam.) B. Øllg. [fide Øllgaard 2012].

GLAZIOU'S LABELS

Up to 370 new taxa have currently been recorded in Glaziou's collection, mainly described by Fée (276) and Baker (51), but also by other botanists:

C. Christensen	9	W.R. Maxon & C.V. Morton	1
H. Christ	8	G.H. Mettenius	1
G.H. Hieronymus	6	K.A.E. Prantl	1
K. Domin	3	E. Rosenstock	1
W.G.F. Herter	3	A. Saint-Hilaire	1
C.A.M. Lindman	3	A.F. Spring	1
G.F. Kaulfuss	2	L.M. Underwood & F.E. Lloyd	1
M. Kuhn	1	C.A. Weatherby	1

As some of the new taxa have been described with the citation of several specimens, the total number of Glaziou's collection recorded to date as syntypes is 475.

Several forms of label have been identified:

- Label from Fée, mostly with his signature (Figure 1);
- Label of duplicates with additional data from Fée and Glaziou (Figure 2);
- Label with uncomplete data written in Glaziou's hand (Figure 3);
- Label bearing one number only:
 - either attached to an axis of the plant by a thread (Figure 4);
 - or with a number written with a blue pen on a piece of brown paper in Glaziou's hand (Figure 5).

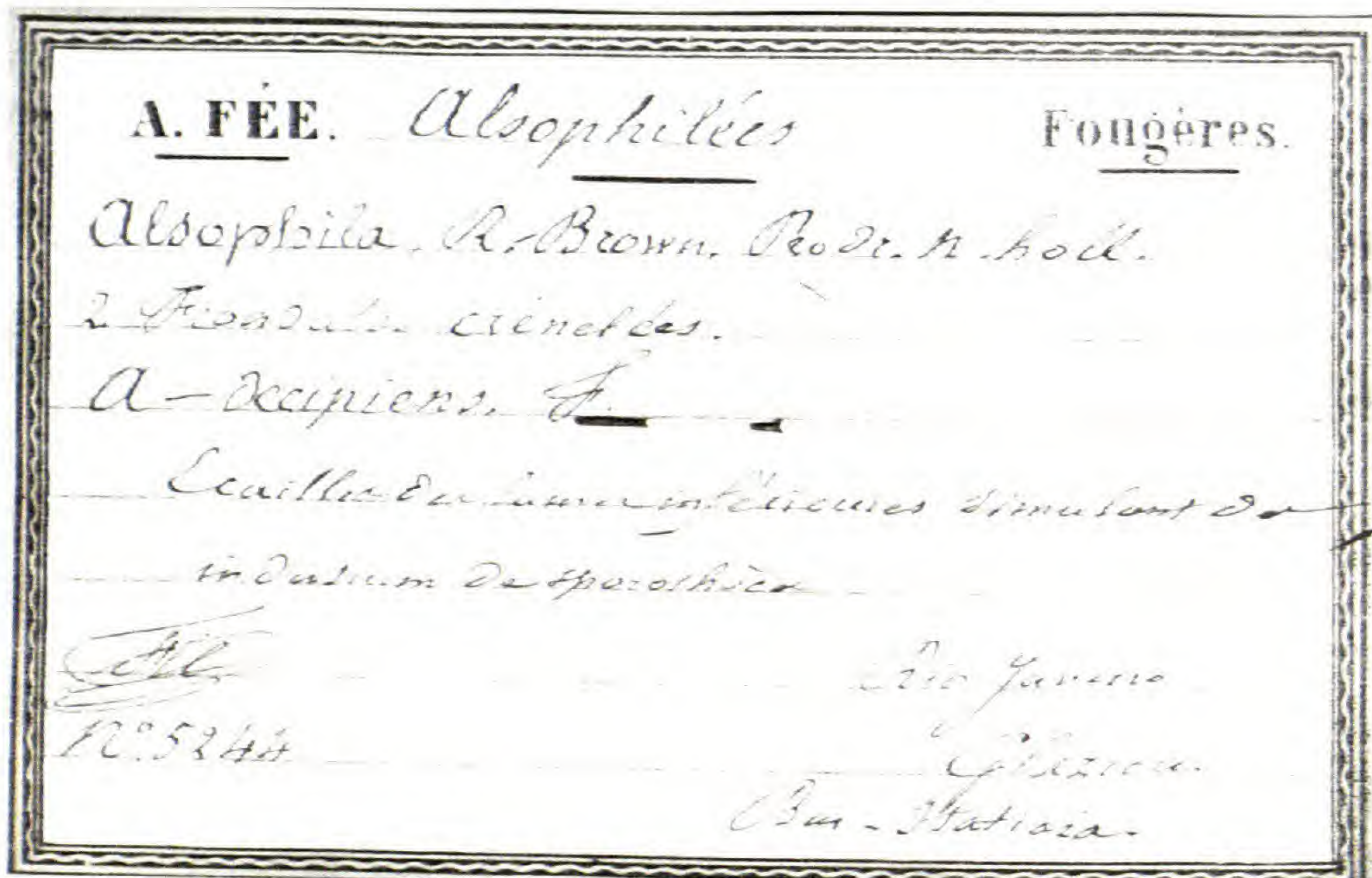


Figure 1. Label written by Fée with his signature: specimen *Glaziou* 5244 (P00625682), syntype of *Alsophila decipiens* Fée.

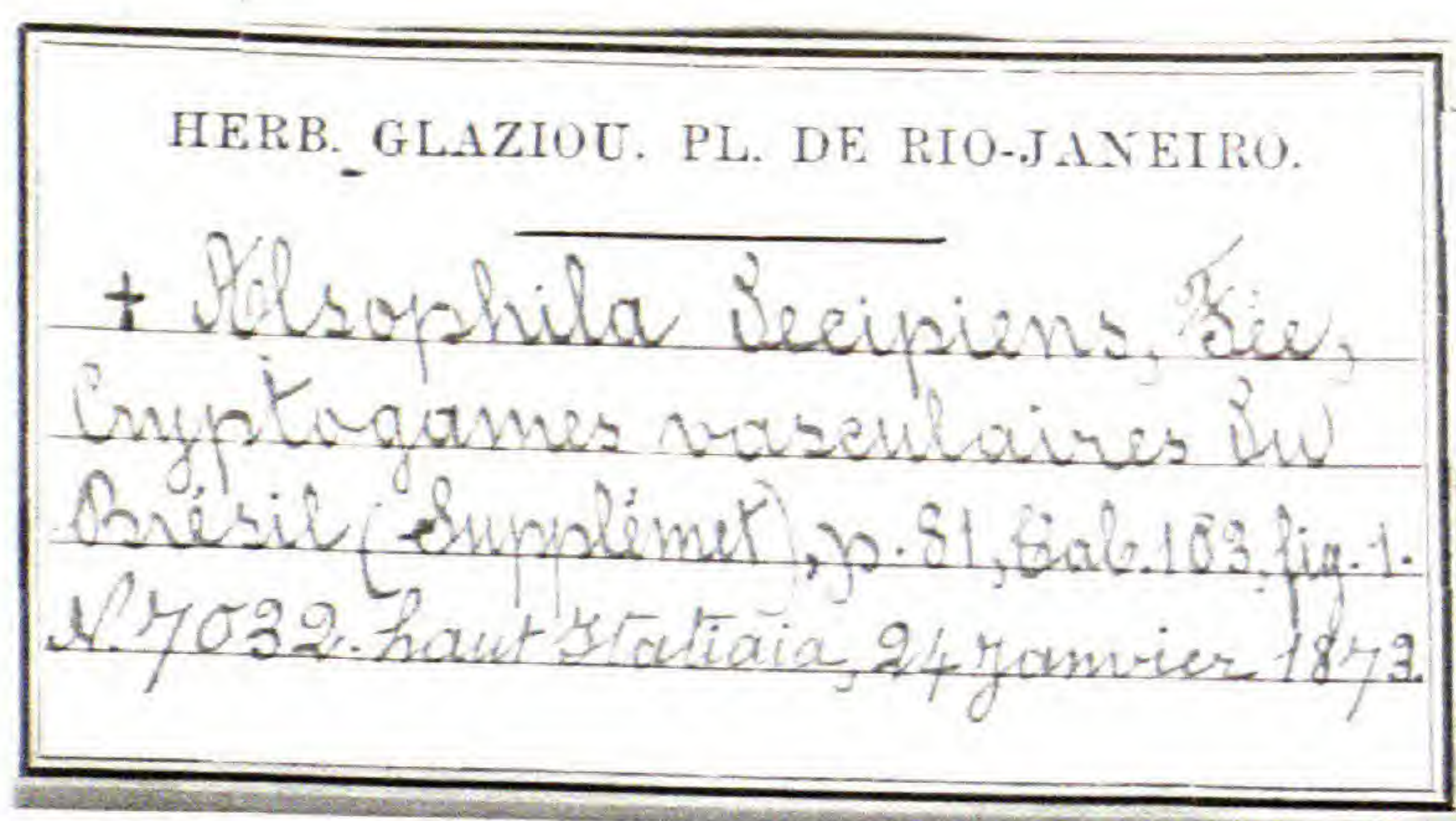


Figure 2. Label written by Glaziou, with various data: specimen *Glaziou* 7032 (P00631702).

Monte La Estacion,
le 10 juillet 1872.
+ Als. decipiens Fée

Figure 3. Label written by Glaziou, with his original data: specimen *Glaziou 5244* (P00625687), isosyntype of *Alsophila decipiens* Fée.

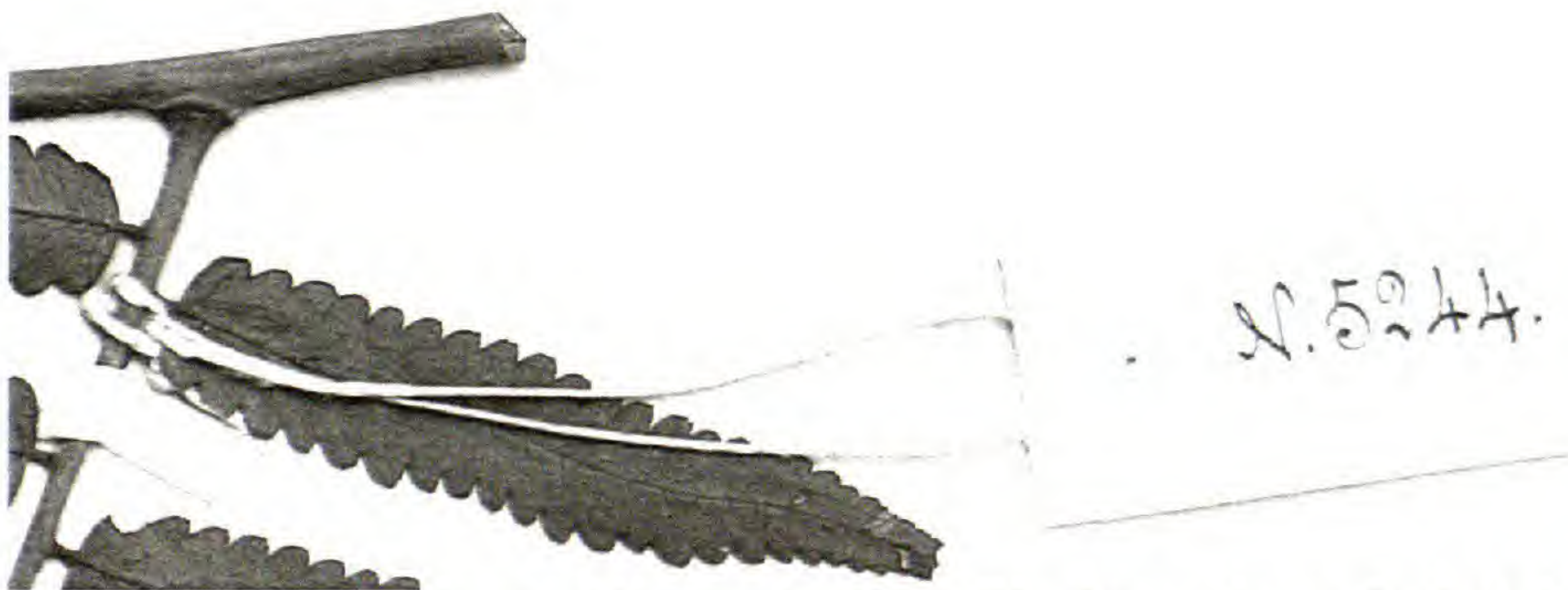


Figure 4. Label of the number 5244, written by Glaziou and attached to the plant by a thread (P00625687).

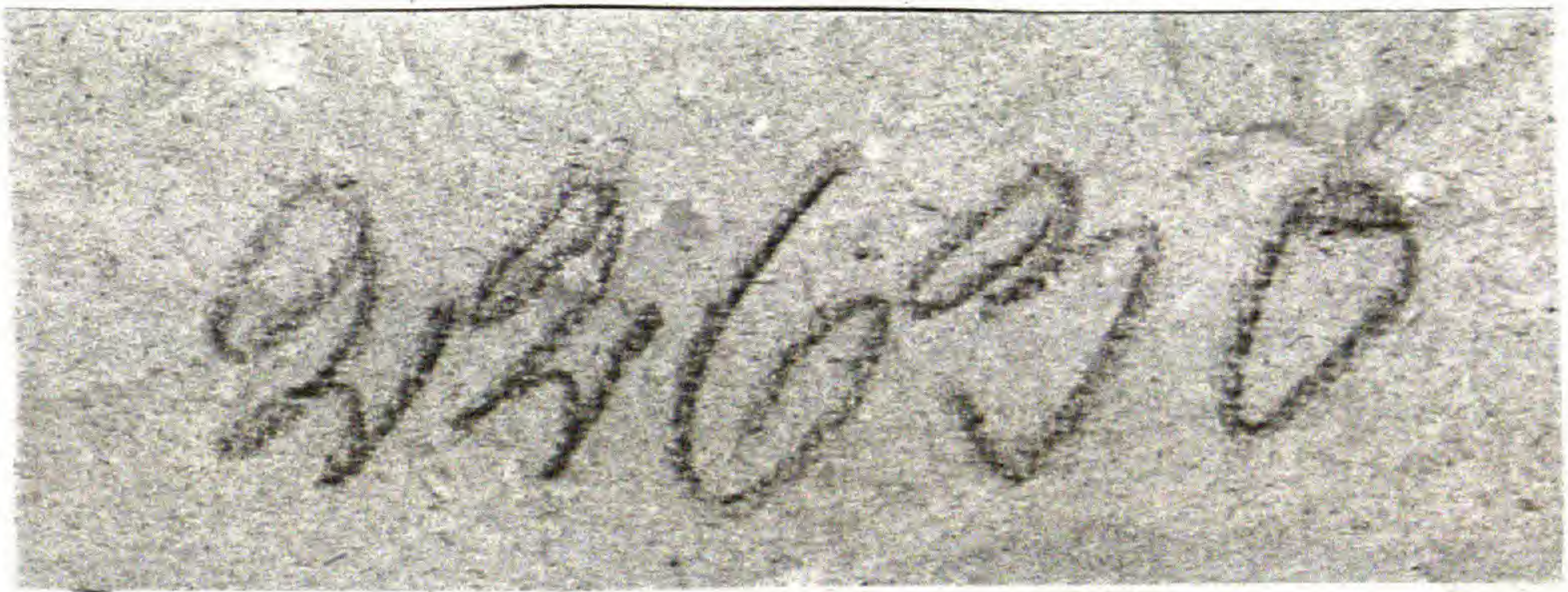


Figure 5. Label of the number 22630, written by Glaziou (P00631772), isotype of *Alsophila goyazensis* H. Christ.

OTHER LISTS ESTABLISHED

List of specimens of Glaziou's collection

As an example of the list that we are compiling, we show the first page in Figure 6.

List of Glaziou's specimens regrouped under the current names of taxa

As an example of how this list is being presented, we show here *Abrodictyum rigidum* (Hymenophyllaceae):

Abrodictyum rigidum (Sw.) Ebihara & Dubuisson

11 CATALOGUE: *Scoparia dulcis* L.
[SCROPHULARIACEAE]

SPECIMEN: Rio de Janeiro: Alto Macahé,
Juillet 1870 (P01541570!)

Heteroneuron serratifolium (Mert. ex
Kaulf.) Fée

CURRENT NAME: *Bolbitis serratifolia*
(Mert. ex Kaulf.) Schott

17 CATALOGUE: *Sophora littoralis*
Schrad. [FABACEAE]

SPECIMEN: Rio de Janeiro: (syn-).

Syntype of *Alsophila leucolepis* Mart. var.
firma Domin

CURRENT NAME: *Alsophila leucolepis*
Mart. var. *firma* Domin

24 CATALOGUE: *Euphorbia sabulicola*
Baill. [EUPHORBIACEAE]

SPECIMEN: Rio de Janeiro: Trannin
(P01248867!)

Doryopteris hastata Raddi

CURRENT NAME: *Doryopteris sagittifolia*
(Raddi) J. Smith

32 CATALOGUE: *Borreria tenella* Cham.
& Schlecht. [RUBIACEAE]

SPECIMEN: Rio de Janeiro: près de Rio de
Janeiro, 1872 (MO-1826063)

CURRENT NAME: *Cyathea delgadii* Sternb.

34 CATALOGUE: *Borreria tenella* Cham.
& Schlecht. [RUBIACEAE]

SPECIMEN: Rio de Janeiro: près de Rio de
Janeiro, 1872 (MO-1856064)

CURRENT NAME: *Cyathea delgadii* Sternb.

39 CATALOGUE: *Beyrichia ocymoides*
Cham. [SCROPHULARIACEAE]

SPECIMEN: Rio de Janeiro: près de Rio de
Janeiro, novembre 1871 (MO-1855168)

CURRENT NAME: *Cyathea microdonta*
(Desv.) Domin

49 CATALOGUE: *Coccoloba populifolia*
Wedd. [POLYGONACEAE]

SPECIMEN: Rio de Janeiro: janvier 1872
(MO-1870292)

CURRENT NAME: *Cyathea phalerata*
Mart.

51 CATALOGUE: *Myrcia recurvata* Berg
[MYRTACEAE]

SPECIMEN: Rio de Janeiro: 1872
(MO-1870306, MO-1823787)

CURRENT NAME: *Cyathea phalerata*
Mart.

61 CATALOGUE: *Byrsonima sericea* DC.
[MALPIGHIACEAE]

SPECIMEN: Rio de Janeiro

In: Polypodium cilare Fée [Crypt. vasc.
Bres. 1869].

CURRENT NAME: *Alansmia reclinata*
(Brack.) Moguel & M. Kessler

65 CATALOGUE: *Myrcia brasiliensis*
Kiaersk. [MYRTACEAE]

SPECIMEN: Rio de Janeiro: près de Rio de
Janeiro, 1872 (MO-1872924)

CURRENT NAME: *Cyathea axillaris* (Fée)
Lellinger

67 CATALOGUE: *Plukenetia tamnoides* M.
Arg. [EUPHORBIACEAE]

SPECIMEN: Rio de Janeiro: 1872
(MO-1870291)

CURRENT NAME: *Cyathea phalerata*
Mart.

68 CATALOGUE: Nothing

SPECIMEN: Rio de Janeiro: Passeio
Publico, 14 mars 1867 (P!)

Craspedaria vacciniifolia (Langsd. &
Fisch.) Link

In: Polypodium vacciniifolium Langsd. &
Fisch. [Fl. Bras. 1(2): 519. 1870]

CURRENT NAME: *Microgramma*
vacciniifolia (Langsd. & Fisch.) Copel.

69 CATALOGUE: Nothing

SPECIMEN: Rio de Janeiro:

In: Polypodium lepidopteris (Langsd. &
Fisch.) Kunze var. *rufulum* (C. Presl)
Baker [Fl. Bras 1(2): 527. 1870]

CURRENT NAME: *Polypodium*
hirsutissimum Raddi

Figure. 6. First page of the list of pteridophyte specimens collected by Glaziou.

- 456** Rio de Janeiro: Corcovado, 2 Sep 1867 (P01304055!)
- 3178** Rio de Janeiro: Petropolis, Serra do Couto, 25 Mar 1869 (P01304056!, S06-1259)
- 7033** Rio de Janeiro: Pic de la Tijuca, 19 Apr 1873 (P01304058!, P01304057!, P01304059!)
- 16646** Rio de Janeiro: (P01304060!, P01304061!, P01304062!, P01304063!)
- s.n.** Rio de Janeiro: Corcovado, 2 Sep 1867 (P01304071!) [prob. N° 456]
- s.n.** (P01304064!, P01304065!, P01304066!, P01304067!, P01304068!, P01304069!, P01304070!).

List of locations of collection classified by date

Here below is the example for the year 1865:

Month	Day	Locality	Number
1865			
January	12	R.J.: Corcovado	372
		R.J.: Serra dos Órgãos, Corcovado	955 c*
	16	R.J.: Corcovado	400
	24	R.J.: Corcovado	386
February	2	R.J. :	978
	8	R.J.: Serra dos Órgãos, Corcovado	956
	13	R.J.: Serra dos Órgãos, Corcovado	436
	14	R.J.: Corcovado	405
	15	R.J.: Corcovado	437
March	12	R.J.: Corcovado	381
	14	R.J.: Corcovado	420
	15	R.J.: Tijuca	931
	18	R.J.: Corcovado	367, 382,
April	25	R.J.: Serra dos Órgãos	916
May	16	R.J.: Gavia	422
	17	R.J.: Corcovado	397
June	7	R.J.: Corcovado	383
	23	R.J.: Gavia	982
July	4	R.J.: Bico do Papagaio	418
	10	R.J.: Lacangueiros	1669
September	10	R.J.: Corcovado	424 c, 450,
	16	R.J.: Corcovado	431
	22	R.J.: Tijuca	950 b
October	5		409
	10	R.J.: Copacabana	449
	18	R.J.: Corcovado	s.n., s.n.,
	22	R.J.: Corcovado	s.n.
November	25	R.J.: Corcovado, à la Tijuca	413
	27	R.J.: Tijuca	392

*Suffixes added by authors

List of taxa having for type a specimen from Glaziou

As an example, here below are given the first three taxa of this list:

- 1. *Acrostichum acuminans*** Fée, Crypt. Vasc. Brésil 1: 12, t.1, f.2. 1869.

PROTOLOGUE: “*Habitat in Brasilia fluminensi, Serra d’Estrella* (H.F.) (Glaziou, n° 951, 2437, 2438, petite forme, et 2469, Alto Macahé, Nova Friburgo).”

LECTOTYPE: BRAZIL: Rio de Janeiro: Serra de Nova Friburgo, 22 May 1868, *A.F. Glaziou* 2438 (lecto- **P00249800!**; isolecto- **BR!**, **P00249801!**, **P00249802!**). Designated by Rouhan & Cremers 2006.

SYNTYPES: BRAZIL: Rio de Janeiro: Serrada Estrella, *A.F. Glaziou* 951 (syn- **P00249803!**; isosyn- **BR!**).

BRAZIL: Rio de Janeiro: Serrada Estrella, *A.F. Glaziou* 2437 (syn- **P00249803!**; isosyn- **K000590644**).

BRAZIL: Rio de Janeiro: Alto Macahé, Nova Friburgo, Jul. 1870, *A.F. Glaziou* 2469 (syn- **P00249804!**; isosyn- **BR!**, **P00249805!**).

= *Elaphoglossum auricomum* (Kunze) T. Moore [fide Smith 1981, Stolze 1981, Mickel & Beitel 1988, Tryon & Stolze 1991, Mickel 1995, Smith 1995, Rojas-Alavarado 2002, Mickel & Smith 2004, Rouhan & Cremers 2006, Funck *et al.* 2007, Hokche *et al.* 2008].

2. *Acrostichum acutum* Fée, Crypt. Vasc. Brés. 2: 9, t.83, f.3. 1873. non Kuhn (1869). *nom. illeg.*

PROTOLOGUE: “*Habitat in Brasilia fluminensi* (Glaziou, n° 5373).”

TYPE: BRAZIL: Rio de Janeiro: Alto Macahé, 10 Jul 1870, *A.F. Glaziou* 5373 (holo- **P00249807!**; iso- **B** 20-0069724!, **MO**-1322125, **P00249808!**, **P00602733!**).

= *Elaphoglossum acutum* (Fée) Brade [fide Pichi Sermolli 1965, Forzza *et al.* 2010].

3. *Acrostichum amplissimum* Fée, Crypt. Vasc. Brés. 1: 5, t.6. 1869.

PROTOLOGUE: “*Habitat in Brasilia, Serra do Ariro* (Glaziou, n° 2436, 1868).”

TYPE: BRAZIL: Rio de Janeiro: Serra do Ariro, 18 Jun 1868, *A.F. Glaziou* 2436 (holo- **P00249820!**; iso- **P00249821!**, **P00249822!**, **P00249823!**).

= *Elaphoglossum amplissimum* (Fée) H. Christ [fide Forzza *et al.* 2010].

THE COLLECTION OF C.F. APPUN (1820-1872)

Born at Bunzlau (Germany) on May 24th, 1820, Carl Ferdinand Appun died in British Guyana on July 18th, 1872. This naturalist was recommended by Alexander von Humboldt to King Frederick William IV of Prussia, who sent him to Venezuela as a botanist. He arrived in this country in early 1849. For about 10 years, he collected plants and animals, notably in the Puerto Cabello, Yaracuy and Cojedes regions, and in the plains of the Orinoco delta. In 1858, he returned to Germany. The following year, the British Government sent him to Guyana where he stayed until 1868. He also visited part of Brazil, notably the Rio Branco and Rio Negro region in Amazonia up to Tabatinga, at the Peruvian border. During his stay in Germany (1868-1871), he published a series of notes in various magazines. In 1871, he returned a second time to Guyana where he died, in 1872, in an accident on the Mazaruni River.

About Appun’s collections, it is known that:

- numerous taxa, new to science, are represented by specimens in this collection;
- his collection from Guyana is made of 401 numbers (i.e. from 199 to 400, then 1419 to 1703), the specimens being deposited mainly in the B, BM and K herbaria;
- his specimens from Venezuela are deposited at BM, K, NY, P (those from LZ having been destroyed during the war);
- his specimens from the Roraima have not been found again, and were thought to have

disappeared.

At P and in other herbaria where a specimen or image has been seen, under the Glaziou's numbering, we have been able to find the following specimens:

12341 GUYANA: *Appun s.n.* (P01403370!) noted as *Acrostichum squamosum* Sw.
= *Elaphoglossum plumosum* (Fée) T. Moore var. *maternum* Mickel [det. J.T. Mickel 1984]
= *Elaphoglossum plumosum* (Fée) T. Moore [fide Cremers & Boudrie 2007].

12344 GUYANA: *Appun s.n.* (P01463383!) noted as *Elaphoglossum simplex* Sw.
= *Elaphoglossum flaccidum* (Fée) T. Moore [det. G. Cremers 2000]

12347 GUYANA: *Appun s.n.* (P01532127!) noted as *Blechnum asplenoides* Sw.
= *Blechnum asplenioides* Sw.

12348 GUYANA: *Appun s.n.* (P!) noted as *Lindsaea guianensis* (Aubl.) Dryand.
= *Lindsaea guianensis* (Aubl.) Dryand. [fide Christ 1899]
= *Lindsaea portoricensis* Desv. [fide Kramer 1957]

NOTE: In B 20-0123954, B 20-0123956, B 20-0123957, this number 12348 is mentioned on the sheets, but Kramer's determination in 1957 is as *Lindsaea stricta* var. *stricta*. The specimen from P will have to be checked again for a final determination when accessible.

12351 GUYANA: *Appun s.n.* (B, BM, BR, C, G, K, LE, P!-4 sheets) noted as *Lindsaea pendula* Klotzsch
= *Lindsaea pendula* Klotzsch [fide Kramer 1957].

12352 GUYANA [as "BRAZIL"]: probably Appun 962 (syn- BM000586177!; isosyn- B 20-0079819, B 20-0079820, C, MPU017978, P00539191!, P00539192!, P00539193!) [det. G. Cremers 1985].
= *Lindsaea semilunata* (C. Chr.) C. Chr. [fide Cremers & Kramer 1991, Kramer 1995, Cremers & Boudrie 2007].

NOTE: This is a syntype of *Lindsaea lancea* (L.) Bedd. var. *semilunata* C. Chr., Bot. Tidsskr. 25: 81. 1902.

PROTOLOGUE: "Glaziou 12352, 12353."

12353 GUYANA [as "BRAZIL"]: probably Appun 962 (syn- P?).
= *Lindsaea semilunata* (C. Chr.) C. Chr. [fide Cremers & Kramer 1991, Kramer 1995, Cremers & Boudrie 2007].

NOTE: This is a syntype of *Lindsaea lancea* (L.) Bedd. var. *semilunata* C. Chr., Bot. Tidsskr. 25: 81. 1902.

PROTOLOGUE: "Glaziou 12352, 12353."

12355 p.p. GUYANA: *Appun s.n.* (P!-3 sheets, B 20-0079836, B 20-0079837) noted as *Lindsaea tetraptera* Kramer
= *Lindsaea tetraptera* K.U. Kramer [fide Kramer 1957].

12355 p.p. GUYANA: *Appun s.n.* (B, G, LE, NY, US)
= *Lindsaea divaricata* Klotzsch

- 12356** GUYANA: *Appun s.n.* (prob. Appun 1259) (**B** 20-0124258, **B** 20-0124259, **BR**, **C**, **G**, **LE**, **NY**, **P!**-3 sheets)
= *Lindsaea pallida* Klotzsch
- 12357** GUYANA : *Appun s.n.* (**B** 20-0079707, **B** 20-0079708, **C**, **LE**, **NY**, **P!**)
= *Lindsaea cultriformis* K.U. Kramer [fide Kramer 1957]
- 12359** GUYANA : *Appun s.n.* (**P**01577977!, **P**01588529!, **P**01588530!), noted as *Lithobrochia pungens* Willd [det. as below by M. Boudrie & G. Cremers in 2013, from scans, P website].
= *Pteris pungens* Willd.
- 12365** GUYANA : *Appun s.n.* (**P!**) noted as *Polypodium marginellum* Sw.
= *Grammitis marginella* (Sw.) Sw. [fide Moran & Riba 1995]. However, the specimen has not recently been seen at P, due to the works at the herbarium, therefore, this uncertain determination needs to be further checked, as *Grammitis marginella* is currently unknown from the Guianas.
- 12370** GUYANA : *Appun s.n.* (**P!**) noted as *Polypodium incanum* Sw.
= *Pleopeltis polypodioides* (L.) E.G. Andrews & Windham [fide Flora of North America 1993, Mickel & Smith 2004, Christenhusz 2009, Forzza *et al.* 2010].
- 12371** GUYANA : *Appun s.n.* (**P**00696802!, **P**00696803!, **P**00696804!) noted as *Polypodium subsessile* Baker
= *Lellingeria subsessilis* (Baker) A.R. Sm. & R.C. Moran
- 12372** GUYANA: *Appun s.n.* (**P**01559788!, **P**01369974!, **P**01369975!) noted as *Hemitelia subincisa* Kunze
= *Cyathea roraimensis* (Domin) Domin [det. M. Boudrie & M. Lehnert 2013, from scan, P website]
- 12373** GUYANA: *Appun s.n.* (**P**01443985!) noted as *Aspidium (Nephrodium) subobliquatum* Baker
= *Cyclodium inerme* (Fée) A.R. Sm. [det. M. Boudrie & G. Cremers 2013, from scan, P website]
- 12374** GUYANA [Brazil]: without loc., *Appun s.n.* (holo- **C**; iso- **B** 20-0040062, **B** 20-0040063, **G**, **P**00630614!) [det. as below by G. Cremers, without date]
= *Cyclodium meniscioides* (Willd.) C. Presl var. *rigidissimum* (C. Chr.) A.R. Sm. [fide Cremers *et al.* 1993, Cremers & Boudrie 2007, Funck *et al.* 2007].
NOTE: Type of *Cyclodium rigidissimum* C. Chr., Bot. Tidsskr. 25: 79. 1902.
PROTOLOGUE: "Glaziou 12374."
- 12375** GUYANA: Guating Cr., *Appun 1032* (holo- **K**000589888; iso- **NY**8640!-fragm., **P**00625671!, **US**00066231-fragm.).
= *Cyathea bipinnatifida* (Baker) Domin [fide Smith 1985, 1995, Cremers & Boudrie 2007].

NOTE: Type of *Alsophila bipinnatifida* Baker, in Hook. & Baker, Syn. fil. ed. 2, 456. 1874.

PROTOLOGUE: "Hab. British Guiana, Appun 1032."

12376 GUYANA: *Appun s.n.* (P01491676!) noted as *Aspidium capense* Willd.
= *Ruhmora adiantiformis* (G. Forst.) Ching [det. M. Boudrie 2013, from scan, P website]

12380 GUYANA: *Appun s.n.* (P01559792!) noted as *Hemitelia multiflora* R. Br.
= *Cyathea cyatheoides* (Desv.) K.U. Kramer [det. M. Boudrie & M. Lehnert 2013, from scan P website]

12388 GUYANA: *Appun s.n.* (P01417237!, P01469405!) [det. as below by D.B. Lellinger in 1989]
= *Trichomanes bicornne* Hook.

12389 GUYANA: *Appun s.n.* (G, P01415518!, P01415519!, P01415526!) noted as *Trichomanes filiforme* Sturm [det. as *Trichomanes cellulolum* Klotzsch by Lellinger in 1989]
= *Abrodictyum cellulolum* (Klotzsch) Ebihara & Dubuisson

12398 GUYANA: 1866, *Appun s.n.* (holo- US00135398-fragm.; iso- P00573996!, P00573997!) noted as *Actinostachys dichotoma* Sw.
= *Schizaea stricta* Lellinger [fide Cremers & Boudrie 2007, Funk *et al.* 2007, Hokche *et al.* 2008, Forzza *et al.* 2010].

NOTE: Type of *Schizaea stricta* Lellinger, Mem. New York Bot. Gard. 18: 8, f.1. 1969.

12399 GUYANA : 1866, *Appun s.n.* (P01593700!)
= *Actinostachys pennula* (Sw.) Hook. [det. M. Boudrie & G. Cremers 2013, from scan, P website]

s.n. GUYANA : gift in 1893, *Appun s.n.* (P01526597 !)
= left : *Trichomanes plumosum* Kunze, likely from upland western Guyana
= right : *Trichomanes accedens* C. Presl [fide Lellinger 1989].

From this list of 24 numbers from the Glaziou collection, we can establish that:

- three specimens only are probably related with the numbering of Appun's specimens (962, 1032, 1259);
- most of Appun's specimens are without a number;
- five specimens are types;
- although no taxon is described by Fée, certain of them are described by Baker (1874), Christensen (1902) and Lellinger (1969).

CONCLUSION

From the current status of our knowledge, we can confirm the historical and taxonomic importance of Glaziou's collection deposited in the herbarium of the National Museum of Natural History in Paris. To date, we have recorded:

- 1,789 specimens of pteridophytes mentioned within his collection catalogue, to which

are added 75 numbers not recorded in the catalogue;

- 370 taxa described new to science, amongst them 276 by A.L.A. Fée and 51 by J.G. Baker.

By very careful examination of the specimens, we have been able to identify the original labels from Fée (and therefore holotypes or lectotypes for the Fée's taxa), and the labels corresponding to duplicates. A more thorough study of the numbers of the collections made at different dates is in progress by referring to the difficulties of interpretation in the formulation of the labels.

Despite the consultation of databases and visits to other herbaria, we have not been able to find again all the numbers mentioned in Glaziou's collection catalogue. Several files and lists have been established preliminarily to facilitate further research. However, a new inventory of the P herbarium will be necessary as soon as the specimens, previously in storage, are incorporated into the new herbarium system.

ACKNOWLEDGEMENTS

We thank the staff of the Paris Museum herbarium (P) and more specially Mrs F. Rakotondrainibe and Mr. G. Rouhan, current curator of the pteridophyte section at the herbarium, for their welcome and their help on site and through correspondence. The collaboration of M. Lehnert (STU, Stuttgart, Germany) in the confirmation of *Cyathea* specimens has been greatly appreciated. We also thank all who participated in building the databases for their invaluable help, as well as Prof. M. Gibby (RBG Edinburgh) for her kind revision of the English text.

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***EQUISETUM* × *SERGIJEVSKIANUM*, A HYBRID HORSETAIL FROM SIBERIA**

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Key words: *Equisetum*, new hybrid, *Equisetum palustre*, *Equisetum pratense*, Siberia, Russia

ABSTRACT

A new hybrid of *Equisetum* L. - *Equisetum* × *sergijevskianum* C.N. Page et I.I. Gureyeva (*E. palustre* L. × *E. pratense* Ehrh.) - was described originally from herbarium material found by the authors in 2007 in Krylov Herbarium (TK, Tomsk State University). *E. ×sergijevskianum* is the first new hybrid in *Equisetum* to be first found in Russia. Presented here is an expanded study in English, giving diagnostic features of this hybrid, comparison with parental species and other hybrids in *Equisetum* subgenus *Equisetum*, and discussion of distribution and ecology of the parental species. This hybrid occurrence endorses that this parental combination can exist, and we suggest that this hybrid could consequently occur elsewhere within the widely-sympatric portions of the circum-boreal ranges of the two parent species, which includes northern Europe, and especially perhaps Scandinavia and northern parts of the British Isles.

INTRODUCTION

In August 2007, an unusual specimen in *Equisetum* L. subgenus *Equisetum* (the 'deciduous' horsetails) was found by the authors in the P.N. Krylov Herbarium (TK) of Tomsk State University (Tomsk, Russia). The specimen in question consisted of two cone-bearing shoots, which had originated from Western Siberia, Russia, collected near Tomsk on 21st July 1925 by Lidia Sergiyevskaya, Maria Kuminova and Elena Vandakurova. Identity of this pair of shoots had long been attributed to *E. palustre* L., and in 1971 this diagnosis was further modified by A.E. Bobrov (as an annotation on the herbarium sheet), clearly recognising its unusual appearance, as *E. palustre* L. var. *verticillatum* Milde f. *longiramosum* Klinge. Our new (Page & Gureyeva, 2009) analysis of its morphological and anatomical details showed the specimen to be far from being typical *E. palustre*, and that it bore instead a uniquely strong intermediacy between *E. palustre* and *E. pratense*. Both of these species are frequent within the region. This evidence thus supports a modern diagnosis of this specimen as the first ever known hybrid between these two species. This new hybrid, *E. palustre* L. × *E. pratense* Ehrh. was thus accordingly described and named *E. ×sergijevskianum* C.N. Page & Gureyeva (Page & Gureyeva, 2009). This is the first new hybrid in *Equisetum* to be first found in Russia, and is named after the original finder of the specimen, who was a well-known Siberian botanist and head of the P.N. Krylov Herbarium (TK) at Tomsk State University from 1931 to 1970.

The present paper presents a fuller account of this interesting hybrid, in a more

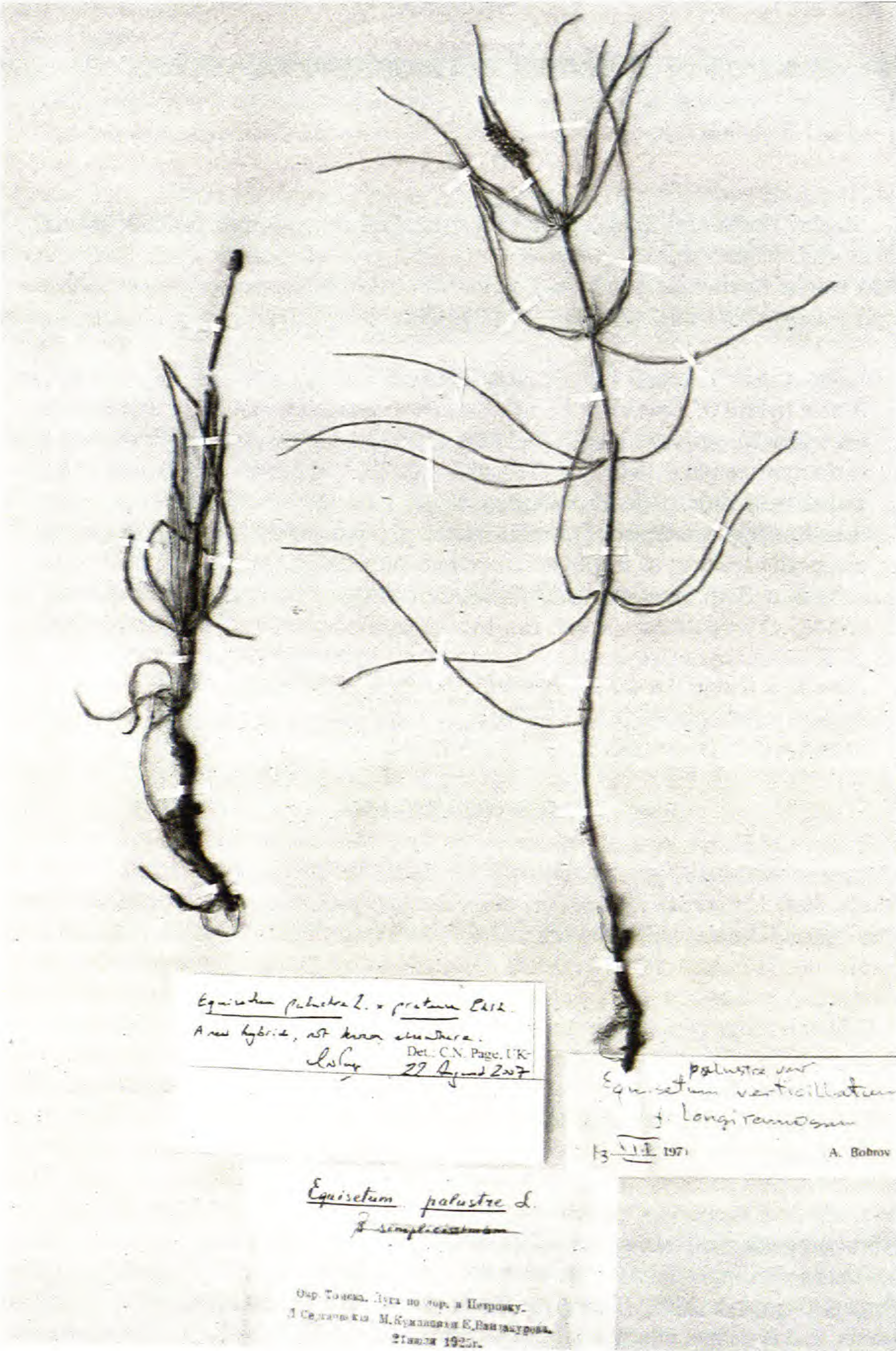


Figure 1. *Equisetum* × *sergijevskianum* C.N. Page et Gureyeva: Whole sheet (holotype, herbarium TK)

accessible form in western literature and to discuss its significance, since, as well as across northern Asia, its two parents are also widespread across both northern Europe and northern North America. This discovery confirms that this hybrid can, indeed, form, and establish sporophyte populations. This hybrid could therefore yet be found elsewhere within the widely-sympatric portions of the circum-boreal ranges of the two parent species, and its description is therefore additionally relevant to studies of both the British and European floras.

DESCRIPTION AND MORPHOLOGICAL NOTES

Equisetum × *sergijevskianum* C.N. Page et Gureyeva (*E. palustre* L. × *E. pratense* Ehrh.), 2009, Sistematičeskie Zametki po Materialam Gerbariâ Imeni P.N. Krylova Tomskogo Gosudarstvennogo Universiteta, 101: 16.

Type description (Page & Gureyeva, 2009): Stems 15-30+ cm, erect, 1.5-2 mm diam., green, with 5-8 grooves and 5-8 ridges; the ridges angular, surface minutely rough; sheaths (excluding teeth) 3.5-5.0 mm, green; teeth 4-5 mm, as many as the ridges, narrowly-triangular, piliferous-acuminate, blackish with wide white scarious margins and acute tips. Branches 1-8 in whorls, spreading to suberect, simple, slender, three angled; ridges acute, the first internode 1.3-2.5 times as short as the corresponding stem sheath; branch sheaths pale, teeth broadly-triangular, acuminate, pale green with narrow scarious margins and top.

Typus: «In the Tomsk adjacents, meadows along the road to Petrovka. 21 July 1925. L.P. Sergiyevskaya, M. Kuminova, E. Vandakurova» (Holotypus TK, Figures 1-3).

Morphological notes on the type material

Equisetum × *sergijevskianum*, in overall habit, presents a relatively small and slender-structured shoot, with a central, simple, more or less erect stem 15-30 cm in length and a lower-shoot diameter seldom exceeding 1.5-2.0 mm. Approximately the lower two thirds of the stem have nodes each bearing whorls of relatively long (up to 6-10 cm), thin (0.6-0.8 mm in diameter) spreading, ascending to sub-erect simple branches. The number of branches per whorl is (1)4-5(8). Thus incomplete whorls occur mostly on nodes of the lowermost part of the stem. The upper one third of the stem is branch-free, and thus forms a prominent 'tail-like' terminal portion to the stem. The resulting general shoot outline of the plant thus varies from narrowly to broadly ovate, and the habit of the plant and the slenderness of both the main shoot and of its long, mostly ascending, branches are prominent initial features, which would be conspicuous and distinctive in the field (Figures 1-3).

In detail, the main shoot internodes have 5-8 acute ridges and the same number of moderately-deep grooves (notably more so than in *E. palustre*). All of the ridges have a minutely rough surface formed by small erect silica tubercles, which can be seen in low-power (eg. x10) magnification, and are particularly prominent immediately below each node through the lower and middle parts of the main stem. Sheaths are green, slightly bell-shaped (in dried herbarium material) with conspicuous ridges. The numbers of teeth and ridges are the same (5-8) as the number of ridges of the internode below. Sheaths are 2 mm in diameter at the base, 3mm in diameter near the teeth and 3.5-5.0 mm in length (without teeth). The 5-8 teeth to each main-stem sheath are free of one another (ie not conjoined), up to 5 mm in length, from dark brown to blackish, narrowly-triangular, broadest at the base, with wide white filmy margins, narrowing down to a relatively long hair-like acute upper portion with (at least in herbarium material) often a

slightly bent tip.

The branches mostly have a 3-fold symmetry, with 3 sharp ridges covered in bead-like tubercles, with narrow grooves between, each with small lengthwise furrows along the base. Branch sheaths are green, with usually 3 erect, thin, forward-pointing (ie. non-spreading, non-clasping), acute, pale-green teeth, 1-2 mm long, sometimes with thin hyaline scarious margins and brownish-tipped teeth. The first internode of a branch is

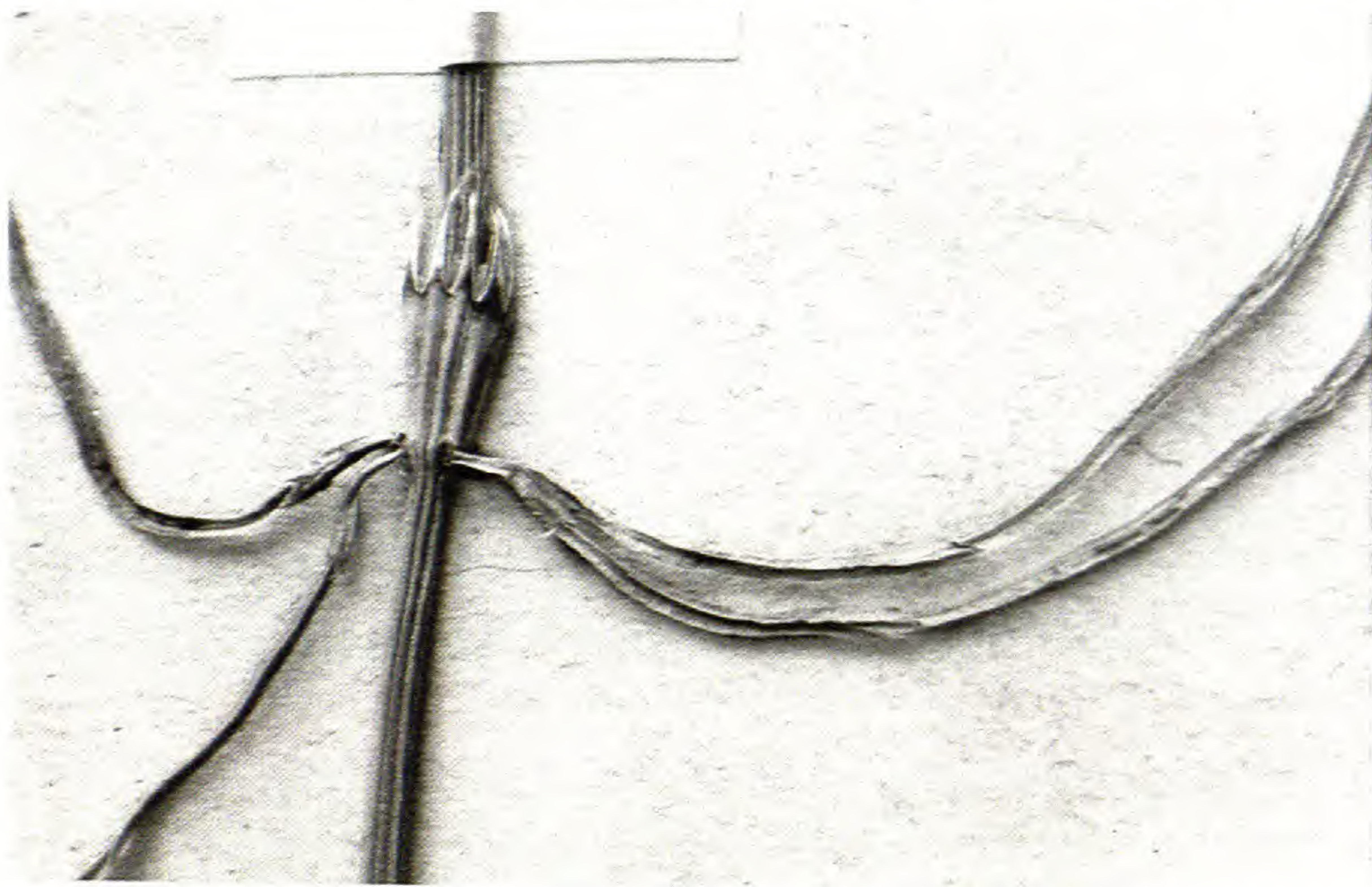


Figure 2. *Equisetum* × *sergijevskianum* C.N. Page et Gureyeva: detail of stem sheath and branches

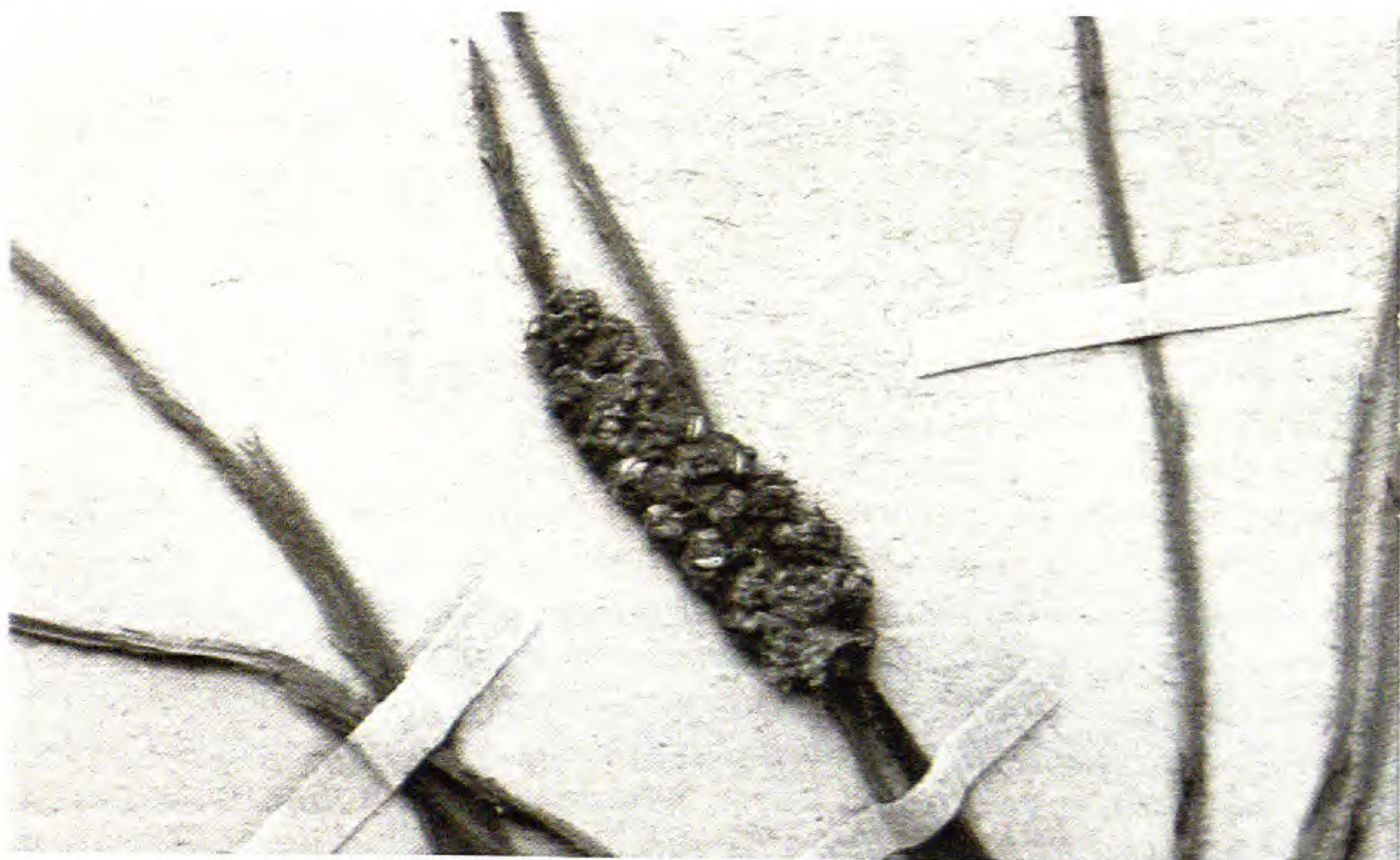


Figure 3. *Equisetum* × *sergijevskianum* C.N. Page et Gureyeva: detail of cone

variable in length, but usually 1.3-2.5 times shorter than the adjacent stem sheath.

On the herbarium sheet, both mounted shoots are fertile (Figures 1 & 3), each with a terminal cone on the otherwise green shoots. The cones are 9 and 15 mm in length respectively. The cones are of somewhat variable shape, ovate (and probably immature) on the smaller specimen, to cylindrical (and apparently fully mature) on the larger specimen, the latter of which has a peduncle 1.5-2 cm in length. Each cone carries 9 whorls of sporangia. The cone of the larger specimen has somewhat congruent terminal sporangia. The spores in both cones are incomplete, corrugated and misshapen.

DISCUSSION

Equisetum × *sergijevskianum* in relation to other hybrids in *Equisetum* subgenus *Equisetum*

Hybrids of horsetails, especially within *Equisetum* subgenus *Equisetum* (the deciduous-shooted horsetails) have now been described in a considerable number of different combinations, particularly within Europe (Page, 1963, 1972, 1973, 1988, 1995, 1997, 2001, 2006; Dines & Bonner, 2002; Lubiensky, 2003, 2010; Page *et al.*, 2007; Page & Gureyeva, 2009; Page, 2012). All characteristically bear a strong morphological intermediacy between the shoot structure of their respective individual parents, and most produce only highly abortive spores, as here, or no cones at all. Significantly, the frequency of recognition of these hybrids, and the number of hybrid combinations known, have increased greatly with time, especially over the last 50 years. Indeed, known hybrids, identified on the basis of morphology, have been subsequently independently supported in their diagnosis on the basis of phenolics (Veit *et al.* 1995), molecular characteristics (Brune *et al.* 2008) and detailed SEM studies (Lubiensky & Doerken 2013).

The present hybrid, *E. × sergijevskianum*, originally described by us from this single specimen from the vicinity of Tomsk, shows a strong morphological intermediacy between *E. palustre* and *E. pratense*, and there is little doubt that it is a hybrid between these taxa. That in the cones of *E. × sergijevskianum* the spores are incomplete, corrugated and mis-shapen, provides further evidence of hybrid diagnosis of this taxon.

Equisetum × sergijevskianum is the fourth described hybrid that has *E. palustre* L. as one parent. Previously described hybrids are *E. × font-queri* Rothm. (*E. palustre* × *E. telmatea* Ehrh.), *E. × dycei* C.N. Page (*E. fluviatile* L. × *E. palustre*) and *E. × rothmaleri* C.N. Page (*E. arvense* L. × *E. palustre*), which are known from many places, at least in Britain (Page, 1997). Like all hybrids of *E. palustre*, *E. × sergijevskianum* shows a strongly intermediate form, in this case of a generally oval outline habit, and ascending branch structure. All the previously described hybrids of *E. palustre* have sterile stems that have a relatively long terminal branchless part. The cones for all hybrids are of intermediate form. All hybrids of *E. palustre* inherit a relatively small number of nodes with relatively long (compared with their width) sheaths. The teeth are fairly broad with scarious margins that become pale when dry. The cones, if present, develop in summer, and tend to be borne atop otherwise green summer shoots.

Equisetum × sergijevskianum is also the fourth described hybrid that has one *E. pratense* Ehrh. as one parent. The previously described hybrids are *E. × mildeanum* Rothm. (*E. pratense* × *sylvaticum* L.), which is known from several locations in Scotland and the mountains of Central Europe (Rothmaler, 1944; Page, 1988, 1997; Lubiensky, 2003), *E. × montellii* Hiitonen (*E. × suecicum* Rothm. (*nom. nudum*), *E. arvense* × *pratense*), which has a very limited distribution in far northern Europe according to Hiitonen (1933) and in Eurasia according to Rothmaler (1944, without further location

data), and *E. × mchaffieae* C.N. Page (*E. fluviatile* × *pratense*), known only so far from one isolated location in Northern Scotland (Page *et al.*, 2007). Like other hybrids of *E. pratense*, *E. × sergijevskianum* has a slender main stem and branches, and detailed stem internode rough micro-structure that clearly indicates the inclusion of *E. pratense* as one parent. Indeed, the obvious roughness of the stem to the touch is a particular character of hybrids with *E. pratense* or *E. sylvaticum* in their parentage. However, *E. × sergijevskianum*, as in other hybrids of *E. pratense*, shows the tops of the teeth in the sheaths of the main stem, at least in its bottom third, to be long, straight, narrow, black, and fully free of one another. The thin branches are angular with a trihedral cross-section, and are simple and unbranched throughout. These characters, and especially the lack of any secondary branching, confirms *E. pratense* is the other parent and not *E. sylvaticum*.

***Equisetum* × *sergijevskianum* in relation to its parental ranges**

The two parents of *E. × sergijevskianum* are each remarkably widespread in the northern hemisphere, especially at high latitudes, and have large areas of geographic overlap.

Equisetum palustre has a range which extends southwards from Arctic Circle and is distributed within Eurasia mainly north of the 40° N parallel, in Europe, from the Pyrenees, northern coast of the Mediterranean Sea, around the Black Sea, in the Caucasus up to the Arctic Circle (eg. Hulten, 1962; Dostal, 1984; Derrick *et al.*, 1987). In Siberia, *E. palustre* is widely distributed within the boreal zone in the North to the Anadyr (Ilyin, 1934; Shaulo, 1988, 2000, 2005; Skvortsov, 2006). It is also present from Mongolia eastwards to Korea and Japan, and southwards to northern and western China, in the latter area occurring as the variety *E. palustre* var. *szechuanense* C.N. Page (Page 1974). In North America it occurs across the temperate zone from the Atlantic Ocean to Alaska, as the variety *E. palustre* var. *americanum* Victorin (Schaffner, 1930; Hauke, 1993). Across at least the western Eurasian part of its range, *E. palustre* is found at a wide range of elevations from habitats below sea level in the far west of Europe up to 2500 m above sea level in the mountainous areas of central Europe (Dostal, 1984; Page, 1988). Its ecological preferences are areas of moist, sandy or marshy soil occurring in waterlogged forests, along the shores of lakes, in marshland, shingle, sandy banks of rivers, thickets of coastal scrub, marine coastal sand dunes, wetland communities with grass, oligotrophic, mesotrophic and eutrophic marshes, especially in northern latitudes (Dostal, 1984; Skvortsov, 2006). In Britain, the species occurs especially in base-rich coastal sand-dune slacks to alpine streamsides, and is an important indicator of cool high level basic flushes (Page, 1988, 1997).

Equisetum pratense has a range which is also circumboreal. In Europe it is present mainly north of latitude 48°N, from Central Europe and the Alps, north to Iceland, Northern Scandinavia and Russia, and continues eastwards at similar latitudes to the Far East, to the Arctic regions of Siberia and Chukotka, southward to Mongolia and China (Ilyin 1934; Jalas & Suominen, 1972; Dostal, 1984; Shaulo, 1988; 2000; 2005; Skvortsov, 2006). It is also present at similarly high latitudes in North America from Alaska to Labrador (Hulten, 1962). Across this vast range, it grows on rich substrates in sparse forests, meadows used for haymaking, on the outskirts of fields, roadsides, on banks of rivers and streams, within open woodlands, thickets and in mountain pastures (Dostal, 1984; Shaulo, 2005; Skvortsov, 2006). In Britain it is noted to grow at moderate to sub-alpine altitudes on moist mineral-rich substrates in the northern parts of these islands, especially on the sandy-clayey banks of rivers and streams, on damp, lightly shaded slopes of valleys, and particularly on flushed streamside sands where a high calcium plus

silica mineral content combine (Page, 1988; 1997; 2001).

That the single sheet of *E. × sergijevskianum* was recognised amongst the herbarium sheets of very many (several hundred) of each of these (above) two parent species examined in the herbarium holding the main plant collections for Siberia, seems to attest to it having a reasonable rarity. That this hybrid has not been previously found, would thus seem not to be a result of lack of frequency of its parent species, nor their areas of overlap, which are hence extremely large in northerly latitudes.

Possible reasons for rarity of *Equisetum* × *sergijevskianum*

Taking an overview of all hybrids in *Equisetum* subgenus *Equisetum*, some hybrid combinations are considerably vigorous, some are about equivalent in vigour to their respective parents, and a few appear to lack any enhanced vigour. Although, in the field, secondary spread of hybrid material by vegetative means has been reported in some hybrid taxa in sites such as along streams and around lakes (Page, 1987; 2001; Page *et al.*, 2007), most newly-occurring hybrid plants, especially where occurring in great isolation, must certainly represent independent *de-novo* hybridisation events (Page & Barker, 1985; Page 2002; Murphy *et al.* 2012). From the frequency of known individuals of some hybrid combinations (eg. *E. × litorale* in Britain and Ireland) these are clearly multiple, though for this hybrid, both numerous *de-novo* occurrences plus additional vegetative spread, appear to exist, and compound to achieve its comparative abundance (Page 1987; 1997). There seems little doubt that, although there may have been some local spread, that the most likely formation of this new Russian hybrid was from a new, *de novo* hybridisation event, involving local outcrossing between gametes from prothalli of each of the two parents identified.

Furthermore, for a great majority of such hybrid combinations, considerable longevity of the resultant offspring, which as judged by the sizes of colonies sometimes formed, probably varies from decades to centuries. This longevity enables such hybrids to often spread and persist long-enough for them to eventually come to botanical notice and analysis (eg Page, 1973; 1995; 2001). We have no direct evidence of the longevity of this particular hybrid. However, impressions in both the herbarium and in the field made by the authors across large swathes of southern Siberia, are that species of *Equisetum*, including the present parents, are widespread and abundant through a great range of forested, woodland, river margin, streamside and lakeside habitats. In the case of the parents of *E. × sergijevskianum*, fieldwork, both within Britain and Russia, shows that they are moderately ecologically separated in more northern and upland regions in particular, and both *E. palustre* and *E. pratense* can occur nearby along margins of streams, each often spreading into streamside sandy gravels. As established sporophyte plants, both species compete well, and appear to have a high longevity, even within relatively dense vegetation, which can rapidly close around them along streambank habitats.

At present, the further ecology of *E. × sergijevskianum* can only be judged by the description on the known herbarium label “meadows along the road”. However it can be expected that the hybrid grows within these in wet, possibly disturbed, patches of intermediate environmental conditions to those of the parental species. In a wider perspective in relation to the parental ecology, knowing that this hybrid can occur, other sites in which it might be especially sought include, we suggest, especially recently-eroded faces of streambanks (even of small rills) and in periodically stream-washed gravel and shingle surfaces. For such sites can provide necessary

recently-disturbed, temporarily opened, adequately wet and irrigated surfaces, for successful prothallial colonisation. Against this background, it is relevant to ask, why this hybrid appears, so-far, to be so scarce. It may have had, or lacked, individual vigour, judging from the relatively small size shoots on the type specimen, when compared with typical sizes of shoots of its parents from the same region, and this may be the cause of its rarity, and possible failure of it to survive long-term.

CONCLUSIONS

This discovery in Siberia is first record of a hybrid between *E. palustre* × *E. pratense*. We suggest that this hybrid could occur elsewhere, perhaps almost anywhere, within the widely-sympatric portions of the circumboreal ranges of its parent species. It is also clearly possible that further study may reveal other hybrids in *Equisetum* from either the Siberian region or across Russia more generally.

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BOOK REVIEW

Ferns, Clubmosses, Quillworts and Horsetails of Cornwall and the Isles of Scilly. **Murphy, R.J., Page, C.N., Parslow, R.E. & Bennallick, I.J. 2012.** Softback, 201pp., ISBN 978-1-902864-07-5. Environmental Records Centre for Cornwall and the Isles of Scilly (ERCCIS), Truro. £20.00

After a gestation period that would have worried an elephant's obstetrician, it was with as much a sense of relief as delight when this attractive treatment of the far south-west's ferns and allies finally arrived. Within the British Isles, Cornwall and the Isles of Scilly have a remarkably rich and varied fern flora, with a range of alien species that have escaped from the long-established gardens for which the region is renowned, and natives such as the Mediterranean *Isoetes hystrix* and *Ophioglossum lusitanicum* unique to this area in the British Isles. Covering over 70 ferns, clubmosses, quillworts and horsetails, their subspecies, varieties and hybrids, both native and introduced, this book, rather like *Welsh Ferns* (Hutchinson & Thomas, 1996) before it, therefore has a broader applicability than its title might suggest.

The major part of the book consists of illustrated taxon accounts: each has a short description of the plant where relevant; the distribution in Europe (including the British Isles); and habitats and distribution in Cornwall and the Isles of Scilly. Maps show distribution by a 2km x 2km square (tetrad) basis in Cornwall, and at a finer resolution (by six-figure grid references) in the Isles of Scilly. The introduction briefly covers the various habitats in Cornwall, the climate, soils and geology and the effects of such activities as mining and china clay workings, and the special conditions on the Isles of Scilly.

The A4 format chosen allows space for the maps to be presented at a good size, along with the many very nice photographs of plant details and habit which make this volume both attractive and useful. The nomenclature and taxonomy are commendably up to date, the only contentious area being the treatment of *Pteridium*, where this author would rather see the subspecies given presented as ecotypes. Even so by presenting these in this fashion more people will become aware of them and our understanding of them can only be improved. The only other observation I would make relates to the account of *Cystopteris fragilis*. All the material that I have seen from Penjerrick is of *C. diaphana* and the status of *C. fragilis* as Cornish, as the text makes clear, is questionable.

This well-produced and very accessible book will, I am sure, do much to encourage an interest in ferns and allied plants and, I hope, may spawn similar regional treatments from elsewhere - it certainly provides a very good model to follow. I warmly recommend it.

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Fred Rumsey

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HOOKE, W.J. 1864. Species Filicum, 5. Dulau & Co., London.

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